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Avicennia (Acanthaceae: Avicennioideae) in North America and Mesoamerica

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A taxonomic revision of *Avicennia*, an acanthaceous genus of mangroves, in North America and Mesoamerica recognizes three species, two native (*A. bicolor* and *A. germinans*) and one locally naturalized in southern California (*A. marina* subsp. *australasica*). Herbarium specimens from throughout the region were used to formulate descriptions of each species, obtain distributional and ecological data, and as a source for pollen in order to characterize and illustrate palynological features of each species. A distribution map, an illustration of the most common species (*A. germinans*), and photos showing diagnostic attributes of each species are provided.

Una revisión taxonómica de *Avicennia*, un género de los manglares en la familia Acanthaceae, en Norteamérica y Mesoamérica reconoce tres especies, dos nativas (*A. bicolor* y *A. germinans*) y una naturalizada localmente en el sur de California (*A. marina* subsp. *australasica*). Los ejemplares de herbario de toda la región se utilizaron para formular descripciones de cada especie, obtener datos distributivos y ecológicos, y como fuente de polen con el fin de caracterizar e ilustrar caracteres palinológicos de cada especie. Además, se ofrecen un mapa de distribución, una ilustración de la especie más comune (*A. germinans*), y fotos que muestran los atributos diagnósticos de cada especie.

Avicennia has been treated previously in several families, most prominent among them Verbenaceae and Avicenniaceae. Molecular phylogenetic analyses (Schwarzbach and McDade 2002; Borg et al. 2008; McDade et al. 2008) and studies of floral structure and development (Borg and Schönenberger 2011) reveal the genus to be monophyletic, nested among Acanthaceae *s.l.*, and sister to either subfamily Acanthoideae or more likely to subfamily Thunbergioideae. The genus is here treated as subfamily Avicennioideae. Although its taxonomic relationships have been controversial, *Avicennia* is well established as a genus of mangrove species. Indeed, they are usually treated in an ecological sense among the so-called "true" mangroves (Tomlinson 1986), which taxa generally occur exclusively in mangrove communities and exhibit both morphological and physiological specializations to the highly saline substrate. It is likely that morphological adaptations to a highly specialized environment have obscured its familial affinities. Other species of Acanthaceae in different tribes of subfamily Acanthoideae are considered to be true mangroves (e.g., *Acanthus ebracteatus* Vahl and *A. ilicifolius* L. of Acantheae *fide* Wang et al. 2011; but treated as mangrove associates by Tomlinson 1986) or mangrove associates (*Bravaisia berlandieriana* (Nees) T.F. Daniel and *B. integerrima* (Spreng.) Standl. of Ruellieae).

The economic importance of mangrove plants in general, and species of *Avicennia* in particular, was correctly pointed out by Moldenke (1960: 144) in citing and refuting another author's statement that plants of *Avicennia* are of little economic importance; Moldenke stated, "…members of this genus are of tremendous economic importance to man and his economy because of their constant battle with the sea and their great success in extending and eventually building up the surface of the land adjacent to the sea in subtropical and tropical climes." Indeed, as discussed by numerous authors (e.g., Tomlinson 1986; Odum and McIvor 1990; Costanza et al. 1997; Chivian and Bernstein 2008; Polidoro et al. 2010; and Cavanaugh et al. 2014) important ecological services provided by mangroves include: serving as home and/or nurseries for numerous marine and terrestrial organisms (e.g., fish, mammals, birds, crustaceans, worms, and insects), protecting coastlines from storm surges (e.g., buffering wave action, preventing flooding and soil erosion, and decreasing saltwater invasion), waste treatment (e.g., nutrient recycling and pollution control), carbon sequestration, and recreation (e.g., eco-tourism and sport fishing). The value of ecosystem services provided by mangrove communities worldwide has been estimated to be at least US $1.6 billion annually (Polidoro et al. 2010). The ecological and economic importance of mangroves, among which several species of *Avicennia* are noteworthy by their abundance and widespread distribution, will only increase with both growth of human populations in coastal areas and sea-level changes associated with climate alterations due to global warming.

Estimates for recent degradation and loss of mangrove vegetation worldwide is significant. Between 20 and 35 percent of mangrove habitats have been lost since about 1980, and the current rate of annual disappearance of this vegetation is estimated to be between one and eight percent (Polidoro et al. 2010). The loss of mangrove communities in Mexico has been estimated as from 15,000 sq. km. in the 1970s to ca. 5,000 sq. km. by the late 1990s (Spalding et al. 1997). Major anthropogenic threats to mangrove communities include coastal development (e.g., tourist/resident infrastructure, mariculture, agriculture, and conversion for harbor/industrial uses), pollution (e.g., sewage effluents, oil spills, and agricultural/industrial/urban runoff), fresh water diversions, and sea level changes due to global warming (e.g., Cintrón M. and Schaeffer N. 1992). For the North American and Neotropical regions, distribution models under future climate scenarios (e.g., Cerón S. et al. 2015) predict a pole-ward shift for mangroves (including *Avicennia germinans*), an overall contraction of species distributions, and a decline in species richness.

This regional taxonomic study used data from more than 650 specimens from North America and Mesoamerica (southern Mexico and Central America) in 22 herbaria to formulate descriptions of species, reproductive phenological periods, distributions, habitats, and other pertinent information. In the few instances where only an image of a specimen was studied, this is noted by "-image!" Pollen from each species was examined with scanning electron microscopy and characterized using terminology of Walker and Doyle (1975). Local names noted herein were obtained from herbarium specimens studied. Many additional local names and uses for these species can be found among references in the literature cited.

Avicennia L., Sp. Pl. 1: 110. 1753; Gen. Pl. ed. 5, 49. 1754. TYPE.— *Avicennia officinalis* L.

Bontia L., Sp. Pl. 2: 638 ("938"). 1753. TYPE.— *Bontia daphnoides* L.
Upata Adanson, Fam. 2: 201. 1763. ≡ *Avicennia* L.
Sceura Forssk., Fl. Aegypt.-Arab. 37. 1775. TYPE.— *Sceura marina* Forssk.
Halodendrum Thouars, Gen. Nov. Madagasc. 8. 1806. TYPE.— *Halodendrum thouarsii* Roem. & Schult.
Hilairanthus Tiegh., J. Bot. (Morot) 12: 358. 1898. TYPE.— Not designated (two species cited).

Shrubs or trees lacking cystoliths and with erect, aerial, and sometimes branched roots (pneumatophores) up to 4 dm tall under and beyond canopy (and infrequently also with aerial stilt roots), cystoliths absent. Leaves opposite, leathery, entire, margin flat to revolute. Inflorescence of axillary and/or terminal dense (sometimes subcapitate) pedunculate dichasiate spikes or panicles of dichasiate spikes; dichasia opposite, 1-flowered, sessile. Bracts ± leathery, concavoconvex. Bracteoles concavoconvex. Flowers sessile, protandrous. Calyx 5-lobed, lobes ± free, concavoconvex, imbricate, equal to subequal in size. Corollas white to yellow to orange, tube expanded distally, shorter than limb, limb 2-labiate or actinomorphic, 4- or 5-lobed, lobes erect to reflexed, oblong to obovate, contorted (left contort aestivation) in bud. Stamens 4, at least 2 exserted from mouth of corolla (in ours), oriented in pairs below upper lip of corolla or oriented symmetrically around corolla with each equally distant from the others; anthers 2-thecous, thecae of a pair ± equally inserted, parallel, ± equal in size, lacking basal appendages, each dehiscing toward lower lip (i.e., flower nototribic) or toward each other (i.e., flower pleurotribic) by a longitudinal slit; pollen suboblate to euprolate, 3-colporate, exine reticulate; staminodes 0. Style not evident or elongating with age of flower; stigma 2-lobed, lobes slightly unequal. Capsule podlike, leathery, ± ellipsoid to ovoid (often asymmetric), ± compressed, unilocular, retinacula absent, dehiscence not explosive, usually occurring at time of detachment or soon after being shed. Seed 1 (–2) per capsule, filling fruit and consisting mostly of ripe embryo with 2 conspicuous folded cotyledons and a pubescent radicle (cryptoviviparous).

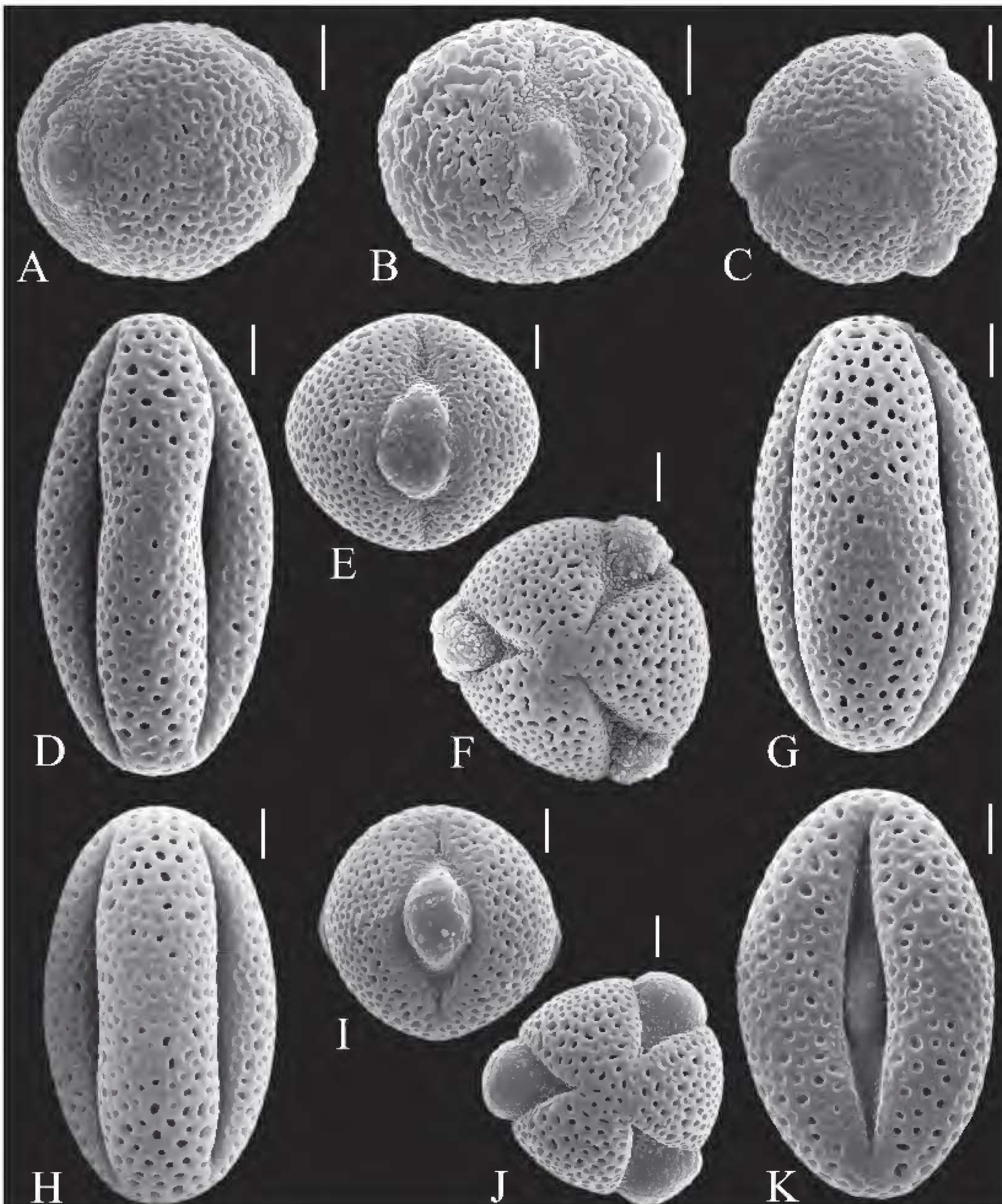
Moldenke (1960, 1973) and Duke (1991) listed additional generic synonyms.

The generic name is derived from Ibn Sina (=Avicenna), 980–1037, a Persian physician, philosopher, and naturalist.

At least eight (e.g., Duke 1991; Duke et al. 1998) species of *Avicennia* are recognized in maritime regions of the tropics and subtropics worldwide. The genus is monophyletic, and includes some of the most prominent and widely distributed "true" mangroves (cf. Tomlinson 1986). Plants occur along shorelines and in tidally influenced waterways in two mostly tropical regions: Atlantic/Caribbean/eastern Pacific (3 spp.) and Indo-western Pacific (5 spp.). Although elevations up to 150 meters have been noted on herbarium labels of American plants, occurrences at elevations much above sea level would appear to be exceptional (if accurately reported) or more likely erroneous. Leaves of *Avicennia* accumulate an external crystalline layer of excreted salt between rains. Three types of major roots are evident on plants: cable roots, anchoring roots, and pneumatophores. Cable roots extend up to several meters horizontally underground from the base of the trunk and give rise to downward growing anchoring roots and upward growing pneumatophores. At least the cable and anchoring roots also give rise to finer roots within the substrate. Pneumatophores (aerial, pencil-like roots that are evident at least at low tide and that facilitate the uptake of atmospheric oxygen) and cryptoviviparous seeds (in which the embryo swells and breaks through the seed coat, but not through the fruit wall, prior to the fruit falling from the plant) are characteristic of the genus. Macromorphological variation among several species of *Avicennia* is extensive, and often has been used in taxonomic circumscriptions. It has been shown that habitat conditions (e.g., variations in salinity and topographic position) and geography can correlate with morphology of the habit, leaves, and/or flowers (Sherrod and McMillan 1985; Duke 1991; Turner et al. 1995). Based on limited sampling (Fig. 1), pollen shape varies from suboblate to euprolate (i.e., with polar diameter:equatorial diameter [P:E] from 0.86 to 1.90). Much of this variation is evident within a single sample (i.e., *Salywon 1188* for *A. germinans*) and probably represents harmomegathic variation.

Key to the Native and Naturalized Species of *Avicennia* in North America and Mesoamerica

1a. Flower actinomorphic; corolla yellowish to orangish, upper lip entire or bifid with the division to 0.2 mm long, the four corolla lobes ovate-triangular to ovate-elliptic; stamens inserted in distal half of corolla tube near base of lobes, oriented equally distant from each other and



dehiscing toward the central gynoecium, 1.5–2 mm long, filaments 0.5–0.8 mm long; naturalized in southern California. . . . . *A. marina* subsp. *australasica*

1b. Flower ± 2-labiate; corolla white to cream (often with yellow in throat), upper lip bifid to 2-parted with the division to 3 mm long, the 4–5 lobes oblong to obovate; stamens inserted at midpoint or in proximal half of corolla tube, oriented in pairs adjacent to upper lip of corolla and dehiscing toward lower lip, 2–5 mm long, filaments 1.5–4 mm long; native in southeastern U.S.A., Mexico, and Central America. 2

2a. Internodes of young stems glabrous; 1-flowered dichasia ± evenly distributed along rachis, internodes near midspike 3.5–7 (–9) mm long, rachis clearly visible; internal surface of corolla lobes glabrous; 2 stamens exserted from mouth of corolla and 2 stamens included in corolla tube (or only partly exserted from it); style not evident after corolla dehisces; capsule blackish when dry. . . . . *A. bicolor*

2b. Internodes of young stems usually scurfy with shiny whitish trichome- or scale-like projections to 0.05 mm long; 1-flowered dichasia congested at or toward apex of rachis (± headlike), internodes near midspike mostly 0.8–4 mm long, rachis not or barely or only partially visible; internal surface of corolla lobes densely pubescent (at least in distal half); all 4 stamens exserted from mouth of corolla; style usually conspicuous after (and often before) corolla dehisces; capsule usually grayish when dry. . . . . *A. germinans*

1. *Avicennia bicolor* Standl., J. Wash. Acad. Sci. 13: 354. 1923. **Type.**— PANAMA: **Coclé**: Aguadulce, outskirts of tidal belt, 5 XII 1911, *H. Pittier 4968* (holotype: US!; isotypes: F-image!, K-image!, BM! NY! P! US!).
Figures 1A–C, 2, 3D.

Shrubs to 3 m tall or trees to 10 (–23) m tall. Young stems of reproductive shoots glabrous (trichomes sometimes persisting around leaf scars, but internodes glabrous). Leaves petiolate, blades ovate to elliptic to broadly elliptic (to obovate), 62–175 mm long, 31–86 mm wide, length:width = 1.2–2.6, (emarginate to) rounded to subacute at apex, rounded to acute to subattenuate at base, surfaces often conspicuously discolorous (abaxial surface lighter), punctate-pitted (sometimes inconspicuously so abaxially), adaxial surface lacking trichomes, abaxial surface covered with a dense scurfy layer that sometimes includes longer ± appressed eglandular trichomes. Inflorescence of axillary (from distalmost leaves) and terminal pedunculate panicles of elongate spikes, panicles ± open, to 115 mm long (including peduncle and excluding corollas) and to 120 mm wide, peduncles 25–40 mm long, glabrous or distally becoming pubescent like branches and rachises, panicle branches subtended by triangular-concave inflorescence bracts (sometimes caducous) 1–3 mm long, pubescent like rachises, fertile portion of spike 12–35 mm long, rachises clearly visible, internodes near midspike 3.5–7 (–9) mm long, densely pubescent with minute (< 0.05 mm long)

Figure 1 (left). Pollen of *Avicennia* spp. A–C. *Avicennia bicolor* (*Sediles 461*). A. Interapertural view. B. Apertural view. C. Polar view. D–G. *Avicennia germinans* (D, *Palmer 484*; E–G, *Salywon 1188*). D. Interapertural view. E. Apertural view. F. Polar view. G. Interapertural view. H–K. *Avicennia marina* subsp. *australasica* (*Moran 28024*). H. Interapertural view. I. Apertural view. J. Polar view. K. Apertural view. Scales = 5 µm.

Pollen measurements (n = number of grains measured, P = polar diameter, and E = equatorial diameter). Many additional grains from each specimen were examined, but data summarized below were made on a subset of those oriented to permit accurate measurements and photographic documentation.

Avicennia bicolor — *Sediles 461* (CAS, n = 5): P = 19–22 µm, E = 19–24 µm, P:E = 0.86–0.92.

Avicennia germinans — *Daniel & Araque 9478* (CAS, n = 2): P = 23 µm, E = 24–25 µm, P:E = 0.92; *de Nevers et al. 6554* (CAS, n = 2): P = 25 µm, E = 26–28 µm, P:E = 0.89; *Palmer 484* (CAS, n = 1): P = 46 µm, E = 24 µm, P:E = 1.90; *Salywon 1188* (CAS, n =4): P = 27–42 µm, E = 24–29 µm, P:E = 0.93–1.75.

Avicennia marina subsp. *australasica* — *Moran 28024* (CAS, n = 4): P = 28–41 µm, E = 24–27 µm, P:E = 1.04–1.70.

glandular trichomes and with antrorse (to flexuose) eglandular trichomes to 0.1 mm long. Bracts triangular-ovate to subcircular, 1–2.3 mm long, abaxially pubescent like rachis. Bracteoles similar to bracts. Flowers mostly 8–10 per spike (but up to 22 per spike). Calyx 2–4 mm long, lobes broadly ovate to subcircular, abaxially pubescent like rachis. Corollas 4.5–7 mm long, internally white to cream, externally glabrous (proximal 2/3 of tube) and densely pubescent with appressed eglandular trichomes to 0.2 mm long (distal 1/3 of tube and limb), tube 2–2.5 mm long, limb ± 2-labiate with 4–5 lobes, upper lip apically 2-parted (with division up to 2 mm long) and/or wider than lobes of lower lip, all lobes oblong to obovate, glabrous internally, 3–4.5 mm long. Stamens 4, inserted at midpoint or in proximal half of corolla tube, 2 exserted from mouth of corolla tube and 2 included in or only partially exserted from corolla tube, oriented in pairs near upper lip of corolla with thecae opening toward lower lip, 2–2.5 mm long, filaments 1.5–2 mm long, anthers presented at 2 heights, thecae 0.3–0.6 mm long; pollen suboblate to oblate spheroidal, polar diameter (P) 19–22 µm, equatorial diameter (E) 19–24 µm, P:E = 0.86–0.92. Style not evident, stigma lobes 0.2–0.4 mm long. Fruit greenish yellow, black when dry, ovoid to ellipsoid, 15–29 mm long, 7–17 mm wide, ± sparsely pubescent with antrorsely appressed eglandular trichomes to 1 mm long, these sometimes more or only evident distally on mature fruits.

Phenology.— Flowering: September–May; fruiting: February–August.

Distribution and habitats.— Pacific coast of southern Mexico (Chiapas, ca. lat. 16°02′26″N), Central America, to southern Panama (Los Santos and Darién, ca. lat. 7.98°N; Fig. 2); plants occur along and near shorelines in coastal mangrove swamps (mangals) and salt marshes at elevations at or near sea level. In addition to the provinces and departments of Central American nations from which specimens have been examined (noted below), this species potentially also occurs or occurred in the following Pacific coastal political units: Guatemala (Escuintla, Jutiapa, Retalhuleu, San Marcos, Santa Rosa, Suchitepequez), El Salvador (La Libertad, La Paz, La Unión, San Miguel, San Vicente, Sonsonate, Usulután), Nicaragua (Carazo, Managua), and Panama (Chiriquí, Veraguas). Gibson (1970) included *Avicennia bicolor* Standl. in her account of the Guatemalan taxa because of its expected occurrence in the country. Although it undoubtedly occurred or still occurs there, the species has yet to be collected in Guatemala.

The southernmost occurrence of *Avicennia bicolor* has been attributed to the Pacific coast of Colombia (e.g., Sanders 1997; Duke 2010; Aymard 2015). The sole collection cited by Aymard (2015; *Forero & Gentry 794* at COL) and another Colombian collection identified as this species (*Gentry & Juncosa 41115* at COL), both appear to pertain to *A. germinans* based on images of these collections supplied by COL. Unless other collections that conform to *A. bicolor* have been made in Colombia, the southern extent of this species appears to be in Panama at ca. 7.98°N, on both sides of the Gulf of Panama (i.e., in the provinces of Los Santos [*Dwyer 5079A*] and Darién [*Duke 5488*]).

Local names.— “Madre sal” (*DeRiemer s.n.*); “madresal prieto” (*Santamaría D. & Romero B. 1a*); “palo de sal” (*Sediles 457*); “palo de sal hoja ancha” (*Sediles 455, 460*).

Conservation status.— The extent of occurrence (EOO) of *Avicennia bicolor* is 262,479 km^2, although a major portion of that area consists of open ocean and inhospitable upland habitats. The species has been assessed as VU (vulnerable) by the IUCN (Duke 2010) based on a documented continuing decline in population under criterion A.

Discussion.— This species is readily recognized by the combination of its glabrous young stems, relatively remote dichasia in the inflorescence (Fig. 3C), bilaterally symmetric flowers with internally glabrous corolla lobes, and black fruits (when dry; Fig. 3D).

The Mexican occurrence of this species has sometimes been overlooked (e.g., Breedlove 1986; Spalding et al. 1997) or minimized (e.g., treated as a synonym of *A. germinans* for practical pur-

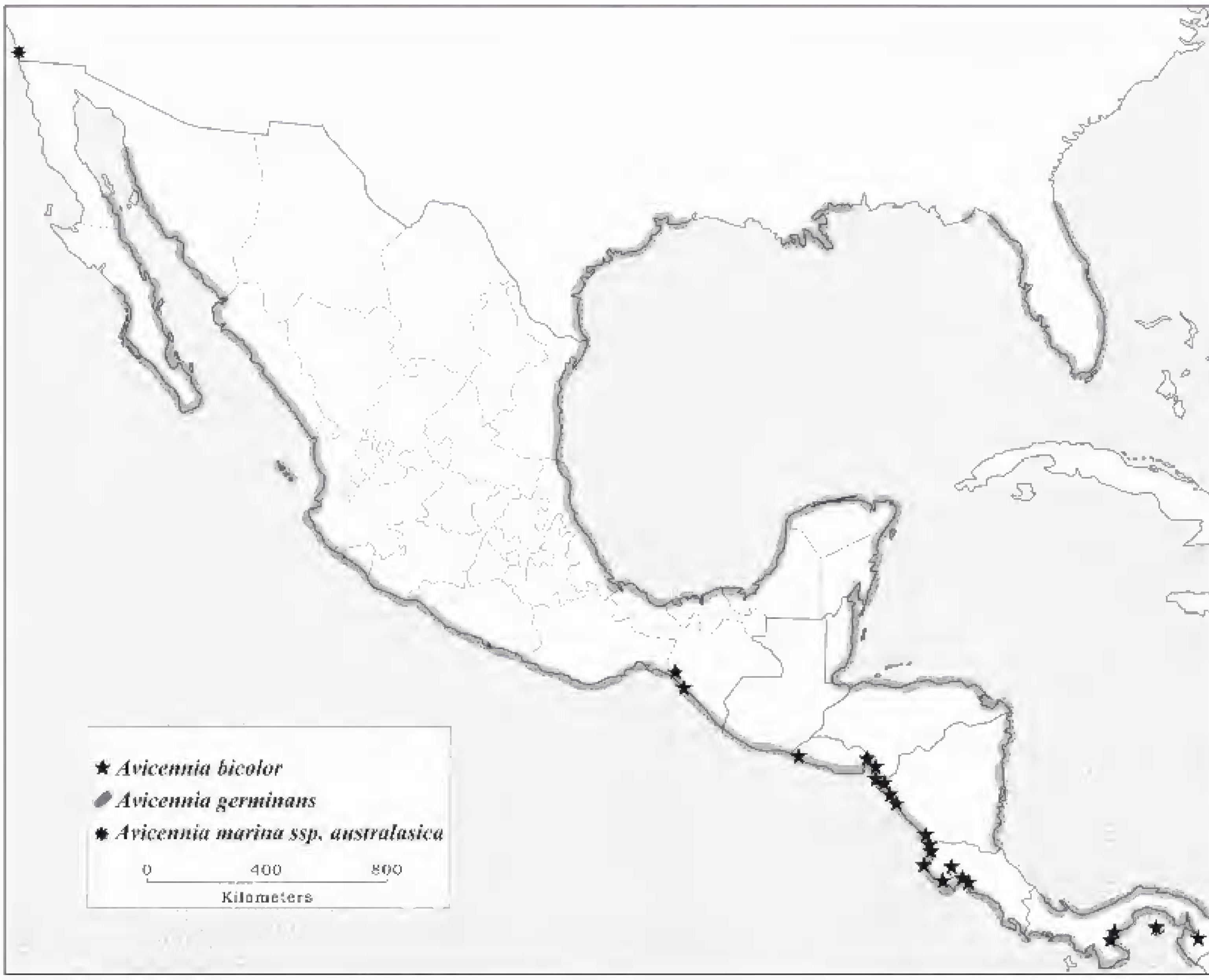


FIGURE 2. Map showing distribution of *Avicennia* spp. in North America and Mesoamerica. The generalized distribution of *A. germinans* is shown. The distribution of *A. germinans* in Cuba and other West Indian islands is not shown.

poses; López P. and Ezcurra 2002). Throughout its distributional range it often grows with *A. germinans* (e.g., *Pittier 4968*, the type, grows with *Pitier 4969*, a collection of *A. germinans* from the same locale). Rabinowitz (1978) noted that where these species are sympatric there is apparently no zonation between them. Like those of *A. germinans*, flowers of *A. bicolor* have been noted to be fragrant (e.g., *Knapp 1244*). Corollas are usually described by collectors as white to cream; they are sometimes noted to have a yellow throat (like *A. germinans*; e.g., Borg and Schöenenberger 2011). *Williams 78* from Panama shows exceptionally long and floriferous inflorescences with the fertile portion of spikes to 65 mm long and with up to 22 flowers (vs. usually 4–8) per spike.

Tomlinson (1986) treated *A. tonduzii* as a synonym of *A. bicolor*, and others have followed his influential taxonomic account (e.g., Aymard 2015). In his key to species of *Avicennia* and description of *A. bicolor*, Tomlinson indicated that corollas of this species were conspicuously pubescent within (as they are on the type of *A. tonduzii*, but not on the type of *A. bicolor*). Distinctions, if any, between *A. tonduzii* and *A. germinans* are not readily apparent, and others have treated these names as synonymous. Additional information about *A. tonduzii* is provided below under *A. germinans*.

ADDITIONAL SPECIMENS EXAMINED.— COSTA RICA. **Guanacaste**: Nandayura, Península de Nicoya, Playa Bejuco, 09°49′56″N, 085°20′34″W, *A. Fernández 1762* (MO); Abangares, Cuenca del Abangares, San Buenaventura, 10°10′29.8253″N, 085°09′31.4524″W, *L. González & A. Garita 3909* (MO); Tamarindo, Playa Tamarindo, 10°18′N, 085°51′W, *W. Haber & W. Zuchowski 8961* (F, MO); Port Parker, *J. Howell 10242* (CAS); Refugio Silv. Tamarindo, Estero Tamarindo, Santa

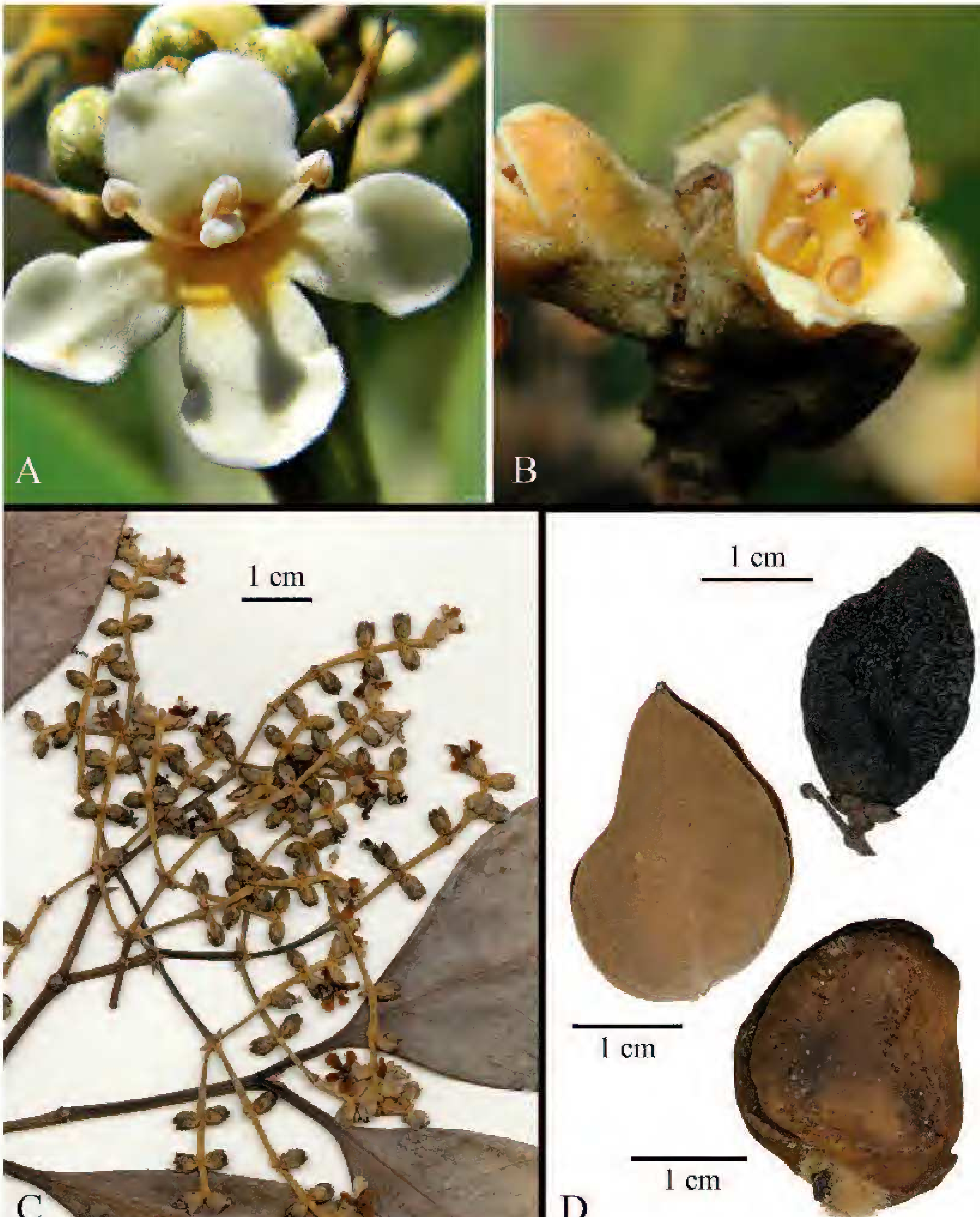


FIGURE 3. *Avicennia* spp. A. Flower of *A. germinans* in Florida (photo by Bob Peterson, cropped, creative commons license, <*https://www.flickr.com/photos/pondapple/7270558948/in/photostream*>). B Flower of *A. marina* subsp. *australasica* in Australia (photo by M. Fagg, cropped, source: Australian National Botanic Gardens at <*http://www.anbg.gov.au/photo*>). C. Inflorescence of *A. biflora* (*Sediles 461*, CAS). D. Fruits of *A. bicolor* (top; *Barrera 8*, CAS), *A. germinans* showing dehiscence (middle; *Ferris 5396*, DS), and *A. marina* subsp. *australasica* (bottom; *Nickerson 6445a* from New Zealand, CAS).

Cruz, 10°19′40″N, 85°49′20″W, *Q. Jiménez 859* (K, MO); P.N. Santa Rosa, Cantón de La Cruz, Península de Santa Elena, Estero Grande, 10°54′59″N, 085°47′03″W, *J. Morales 4142* (F, MO); P.N. Santa Rosa, Playa Naranjo, 10°47′53″N, 085°40′44″W, *J. Morales et al. 1262* (F); Puerto Jesús, *R. Pohl & G. Davidse 10588A* (F, MO, US); Cantón La Cruz, P.N. Santa Rosa, Peninsula de Santa Elena, Murciélago, 10°55′20″N, 85°44′15″W, *F. Quesada 84* (K, MO); P.N. Santa Rosa, Playa Naranjo, *N. Zamora et al. 1140* (F, MO). **Puntarenas**: Golfo de Nicoya Externo, Isla San Lucas, Punta Cañón, *J. Morales & D. Santamaria 12387* (MO); Garabito, Cuenca del Jesús María, Garabito, alrededores de Playa Punta Loros, 09°51′26.3900″N, 084°41′29.8110″W, *A. Rodríguez & V. Ramírez 6688* (MO).

El Salvador. **Ahuachapán**: without locale, *Padilla 333* (US); Las Salinas, *K. DeRiemer 1625* (US), *1626* (US); Las Chacaras, en La Barra de Santiago, *K. DeRiemer s.n.* (US).

Honduras. **Choluteca**: Playas de Cedeño, *F. Padilla 101* (BM). **Valle**: Puerto Soto, 12 km from El Tular, *A. Molina R. 21457* (BM, NY, UC, US); Puerto Soto, 15 km WSW de San Lorenzo, *C. Nelson 1323* (MO).

Mexico. **Chiapas**: Paderón, Tonala, *E. Matuda 16353* (US); Mpio. Pijijiápan, Estero San José, 15°43′39.50″N, 093°29′50.20″W, *S. Santamaría-Damián & E. Romero-Berny 1a* (MEXU), *1b* (MEXU).

Nicaragua. **Chinandega**: Mpio. El Viejo, Reserva Natural de Cosigüina, San Remigio entre El Congo y Bella Vista, 13°01′N, 097°35′W, *I. Coronado G. & R. Rueda 3626* (MEXU, MO); Mpio. Puerto Morazán, de Morazán hasta 5 km en dirección Ttonalá, 12°49′N, 087°09′W, *R. Rueda et al. 17322* (MEXU, MO). **León**: Isla del Venado, 3.3 km de Las Peñitas, *Barrera 8* (CAS); Las Peñitas, Isla Juan Venado, 12°13′N, 086°53′W, *I. Coronado G. & R. Rueda 4943* (MO); Las Peñitas, Isla Juan Venado, 12°17′N, 086°53′W, *I. Coronado G. et al. 6979* (MO); Isla del Venado, 8.2 km de Las Peñitas, 60 m del Estero Las Peñitas, *Sediles 445* (NY), *456* (NY); 3.3 km de Las Peñitas, Isla del Venado, *Sediles 454* (MO), *459* (MO), *461* (CAS); 3 km de Las Peñitas, en la Isla del Venado, *Sediles 455* (F), *460* (K); 8.1 km de Las Peñitas, en la Isla del Venado, 60 m del Estero Las Peñitas, *Sediles 457* (P); 8.3 km del Las Peñitas, en la Isla del Venado, 80 m del Estero Las Peñitas, *Sediles 458* (US). **Rivas**: "Marsella," 11°16–17′N, 85°52–53′W, *M. Araquistain 3828* (MO, P); San Juan del Sur, entre Las Playas de Marsella y Rivas, 11°17′N, 085°54′W, *R. Rueda et al. 1435* (MO).

Panama. **Coclé**: ca. 2 km del Puerto, camino entre el puerto de Aguadulce hasta el pueblo, *M. Correa A. 4314* (MO); Isla del Pozo, salinas of Río Estero Salado, 08°11′N, 080°30′W, *S. Knapp et al. 3401* (MEXU, MO); below Aguadulce, *E. Tyson 7262* (FSU, MO). **Darién**: ca. 10 mi S of El Real on Río Pirre, *J. Duke 5488* (MO). **Herrera**: Cienega El Mangle, NE of Paris, *S. McDaniel 8020* (FSU, MO). **Los Santos**: Monagre Beach, *J. Dwyer 5079A* (MO). **Panamá**: Isla Casaya, J. Duke 10372 (MO); San José Island, ca. 55 mi SSE of Balboa, Playa Grande, *I. Johnston 1259* (DUKE, MO, P, US); Porto Posada, *R. Williams 78* (NY). **Panamá Oeste**: Punta Chame, *W. D'Arcy 10241* (MO); Punta Chame, 10–15 mi from Pan American Hwy., 08°40′N, 079°45′W, *S. Knapp 1244* (MEXU, MO).

2. *Avicennia germinans* (L.) L., Sp. Pl., ed. 3, 2: 891. 1764. *Bontia germinans* L., Syst. Nat., ed. 10, 2: 1122. 1759. Type.— "Habitat in Indiis" [JAMAICA], *P. Browne s.n.*, LINN Herb. No. 813.2 (lectotype, designated by Stearn [1958: 35]: LINN-image!).
Figures 1D–G, 2, 3A,D.

Avicennia nitida Jacq., Enum. Syst. Pl. 25. 1760. *Avicennia officinalis* var. *nitida* (Jacq.) Kuntze, Revis. Gen. Pl. 2: 502. 1891. *Hilairanthus nitidus* (Jacq.) Tiegh, J. Bot. (Morot) 12: 358. 1898. Type.— See discussion.

Avicennia tomentosa Jacq., Enum. Syst. Pl. 25. 1760. *Hilairanthus tomentosus* (Jacq.) Tiegh, J. Bot. (Morot) 12: 358. 1898. **Type.**— See discussion.

Avicennia tomentosa Jacq. var. *campechensis* Kunth, Nov. Gen. Sp. 2: 229 (ed. folio); 284 (ed. quarto). 1818 ("1817"). **Type.**— MEXICO. **Campeche**: "Crescit prope Campeche Mexicanorum," *F. Humboldt & A. Bonpland s.n.* (holotype: P-P00670135-image!).

Avicennia floridana Raf., Atlantic J. 1: 148. 1832. **Type.**— Not designated (no specimens cited).

Avicennia floridana Gand., Bull. Soc. Bot. France 65: 64. 1918, nomen illegit. **Type.**— U.S.A. **Florida**: Lee County, Fort Meyers, *A. Hitchcock 270* (see discussion).

Avicennia oblongifolia Chapm., Fl. South. U.S. 310. 1860. **Type.**— U.S.A. **Florida**: Monroe County, Oct, Key West (fide protologue); pertinent specimens, if extant, would likely be in the Chapman herbarium at NY, but none have been located.

Avicennia tonduzii Moldenke, Phytologia 1: 273. 1938. **Type.**— COSTA RICA. **Puntarenas**: Punta Mala [ca. 09°03′54.48″N, 083°39′04.84″W], zone littorale du Pacifique, Mar 1892, *A. Tonduz 6776* (holotype: BR-image!, fragment of holotype at NY!; isotypes: BM-image!, M-image!, MICH-image!, US!).

Shrubs to 5 m tall or trees to 20 (–25) m tall. Young stems of reproductive shoots covered with dense ± antrorsely appressed or matted whitish and shiny trichomelike or scalelike projections to 0.05 mm long (scurfy) and sometimes also with longer appressed eglandular trichomes, the internodes infrequently glabrate. Leaves petiolate, blades narrowly to broadly elliptic (to obovate), 25–160 (–185) mm long, 11–50 (–63) mm wide, (1.6–) 2.7–6.9 × longer than wide, acute to rounded to emarginate at apex, acute to subattenuate at base, surfaces often conspicuously discolorous (abaxial surface lighter), punctate-pitted (sometimes inconspicuously so abaxially), adaxial surface lacking trichomes, abaxial surface covered with a dense scurfy layer that includes ± appressed longer eglandular trichomes or sparsely to densely scurfy without longer trichomes. Inflorescences of axillary and terminal pedunculate densely bracteate (± headlike) spikes or panicles of these, inflorescence branches (if present) subtended by triangular- to oblate- to subovate-concave inflorescence bracts to 5 mm long (sometimes caducous), peduncles (5–) 10–50 mm long, scurfy, pairs of flowers congested at or toward apex of rachis, inflorescence internodes mostly 0.8–4 mm long near midspike, rachis not or only partially or barely visible, densely pubescent with mostly antrorse eglandular trichomes to 0.2 mm long. Bracts triangular to oblate to broadly ovate to subcircular, 1–4 mm long, abaxial surface scurfy to pubescent like rachis. Bracteoles similar to bracts. Flowers 8–14 (–26) per spike. Calyx 2–4 mm long, lobes broadly ovate to subcircular, abaxially pubescent with antrorsely appressed eglandular trichomes to 0.4 mm long. Corollas (3.5–) 4–8 mm long, internally white to cream with yellow in throat, externally glabrous (proximal portion of tube) and densely pubescent with appressed eglandular trichomes to 0.5 mm long (distal portion of tube and limb), tube (1.5–) 2–3.5 mm long, limb ± 2-labiate with 4 or 5 lobes, upper lip bifid to ± conspicuously 2-parted at apex (with division up to 3 mm long) and/or wider than lobes of lower lip, all lobes oblong to obovate, densely pubescent (at least on distal half if not throughout) internally. Stamens 4, inserted at midpoint or in proximal half of corolla tube, exserted from mouth of corolla tube, oriented in pairs near upper lip of corolla with thecae opening toward lower lip, 3–5 mm long, filaments 2.2–4 mm long, anthers presented at ± same height, thecae 0.6–1 mm long; pollen oblate spheroidal to euprolate, polar diameter (P) 23–46 µm, equatorial diameter (E) 24–29 µm, P:E = 0.92–1.90. Stigma lobes (0.2–) 0.4–0.7 mm long. Fruit ovoid to broadly elliptic to obovoid, usually grayish (rarely black) when dry, 12–32 mm long, 9–25 mm across at widest expanse, pubescent with antrorsely appressed eglandular trichomes to 0.7 mm long (especially when less mature) and scurfy (especially when more mature).

Phenology.— Flowering: throughout the year; fruiting: April–January (especially in August, and likely throughout the year).

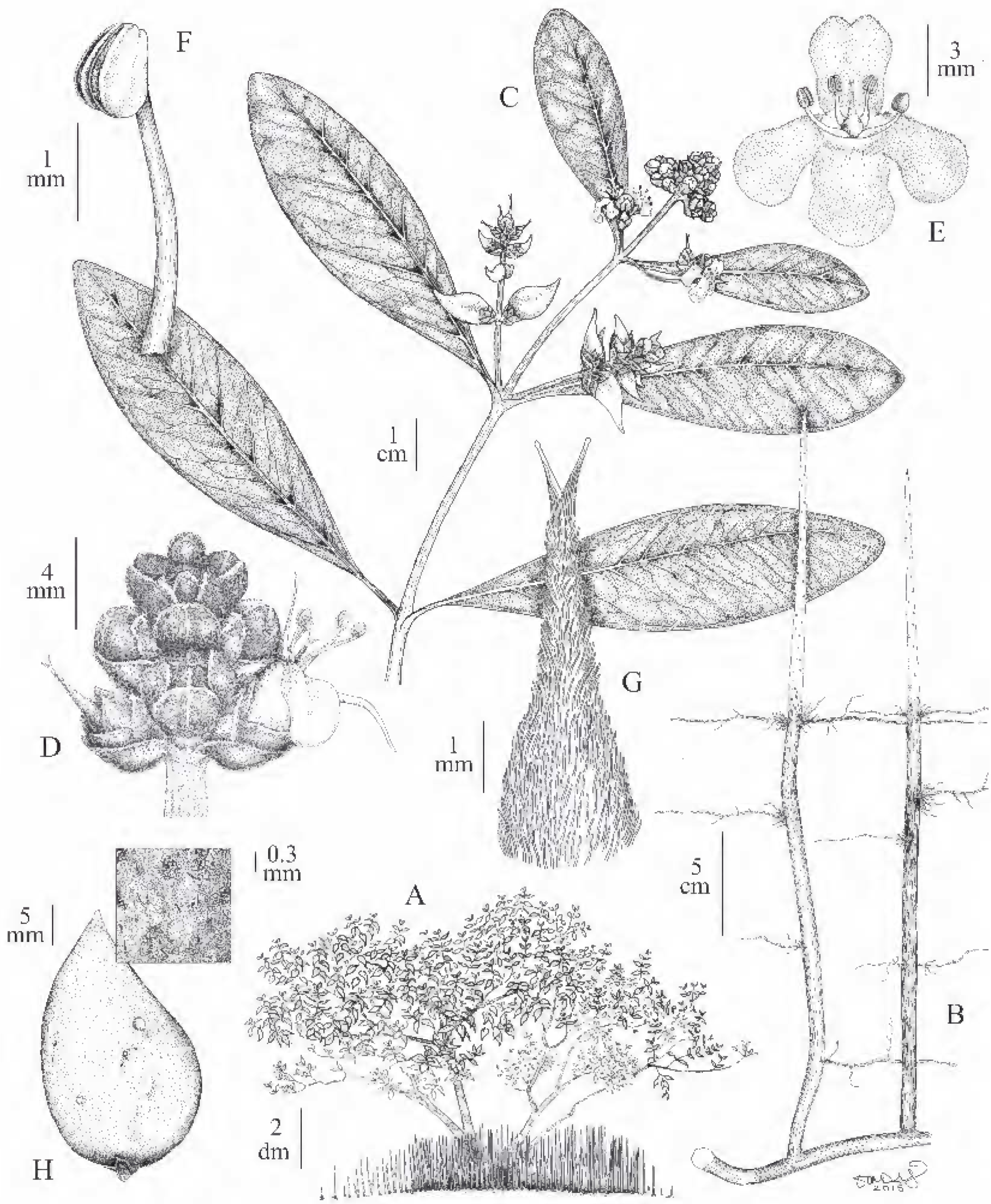


FIGURE 4. *Avicennia germinans*. A. Habit (composite from photos of living plants). B. Pneumatophore (*Schwartz & Nickerson 9119*). C. Fertile shoot (*Calzada 434*, *Pipoly 9034*, *Sousa 3112*). D. Inflorescence with flower in profile (*Lakela 29824*, *Sousa 3112*). E. Flower, front-view (*Lakela 29824*, *Sousa 3112*). F. Stamen (*Sousa 3112*). G. Gynoecium (*Lakela 29824*). H. Fruit with detail of surface (*Lundell 7009*). Drawn by Tom Davis from specimens at CAS.

Distribution and habitats.— Southern North America (southeastern USA and Mexico), Bermuda, West Indies, Central America, South America (Brazil, Colombia, Ecuador [including Galapagos Islands], French Guiana, Guyana, Peru, Surinam, and Venezuela), and tropical western Africa (see Daniel and Figuerido [2009] for distributional information on African plants, which often have been referred to as *A. africana* P. Beauv.). Figure 2 shows the generalized distribution of this species in North America and Mesoamerica. Plants occur in/on tidal flats, beaches, coastal mangrove swamps (mangals), salt marshes, sand dunes, and coastal grasslands and savannas at elevations at or near sea level. Common associates include *Allenrolfea occidentalis*, *Batis maritima*, *Bravaisia berlandieriana, Coccoloba uvifera*, *Conocarpus erectus*, *Distichlis litoralis*, *D. spicata*, *Echinochloa polystachia*, *Frankenia palmeri*, *Laguncularia racemosa*, *Maytenus phyllanthoides*, *Rhizophora mangle*, *Salicornia biguelovii*, *S. virginica*, *Scaevola plumieri*, and *Spartina alterniflora*.

Avicennia germinans is the most widely distributed species of *Avicennia* in the New World. Its northern distributional limit there is in Bermuda (ca. 32°20′N; Lacerda et al. 2002), where another true mangrove, *Rhizophora mangle* L. also attains the northern extent of its distribution; these occurrences are the northernmost of true mangroves. The northernmost occurrence of *A. germinans* on the Atlantic Coast of North America is in northern Florida (St. Johns County, 30°06.618′N, 081°22.303′W, *Williams & Eastman s.n.* at USF). On the coast of the Gulf of Mexico the northern extent of the species extends as far as the Bay St. Louis, Mississippi (Hancock or Harrison county, ca. 30°2′N, *Sanger s.n.* at NY).

Of the three true mangroves that are common on the American mainland (*A. germinans*, *Laguncularia racemosa*, and *Rizophora mangle*) *A. germinans* is the northernmost in distribution. Its northern limit in North America appears to be determined by the frequency and duration of subfreezing temperatures, which can kill the above-water parts of the plants or cause mortality (Sherrod and McMillan 1985; Cavanaugh et al. 2014). Tomlinson (1986) noted a close correlation of the limits of the distributions of mangroves with the 24° isotherm of sea surface temperatures. A decade later Rützler and Feller (1996) indicated that like corals, mangroves cannot survive where an average water temperature falls below about 23°C. In recent decades, freeze-free winters have led to an expansion of *A. germinans* into salt marshes at the northern extremes of its range in the southern United States (Guo et al. 2013). A poleward expansion of the distributional range of *A. germinans* in southern North America, likely correlated with warmer winter temperatures and less extreme freezes, was recently noted by Cavanaugh et al. (2014).

In the United States, plants have been documented from most of the coastal counties in Florida (except for most of those in the panhandle on the Gulf Coast in the northwestern portion of the state), rarely reported from at least two of the three coastal counties in Mississippi (e.g., Moldenke 1960; Scheffel et al. 2014; the locality cited for Mississippi by Lowe in 1921, Door Point, is in Louisiana), and documented from seven coastal parishes in Louisiana. In Texas the species has been collected along the Gulf Coast from Jefferson County near the Louisiana border intermittently southward to Cameron County on the Mexican border. Although it likely occurs (or occurred) in all coastal counties of Texas, based on specimens noted below and in literature reports (Turner et al. 2003 and pers. comm. in 2010 from updated but unpublished maps; Rosen and Zamirpour 2014), it has been collected in Aransas, Brazoria, Calhoun, Cameron, Galveston, Jackson, Jefferson, Kleberg, Nueces, Refugio, San Patricio, and Willacy counties. Sherrod and McMillian (1981, 1985) discussed the distributional history of mangroves, including *A. germinans*, in Texas and in the northern Gulf of Mexico. The species has not been reported from the Gulf coast of Alabama (e.g., Kral et al. 2011).

Avicennia germinans is known from all 16 coastal states of Mexico (occurring along the Gulf of Mexico, Caribbean Sea, Pacific Ocean, and Gulf of California). The species reaches its northern extent in western Mexico along the Gulf of California in Sonora (Puerto Lobos, lat. 30°15′N; Felger et al. 2001) and its northern extent on the Pacific coast in Baja California Sur (ca. lat. 26°N; Turner et al. 1995). Distribution along Pacific coast of North America does not extend as far northward as that along the coasts of the Gulf of California, Gulf of Mexico, and the Atlantic Ocean likely because of upwelling of cold waters off the western coast of the peninsula of Baja California and California that limits their northward spread. Turner et al. (1995) discuss the distributions and probable environmental factors effecting them for this species in regions around the Gulf of California.

In Central America to the south of Belize, the extent of mangrove communities and the abundance of *A. germinans* are better developed along the Pacific than the Caribbean coast. Indeed no specimens have been seen from the Caribbean coast of Costa Rica, although *A. germinans* has been reported from the mouth of the Río Moín, north of Puerto Limón (Zamora et al. 2004). In South America, as in North America, *A. germinans* has a broader distribution on the Atlantic than on the Pacific coast. Lacerda et al. (2002) indicated that the southernmost occurrences of *A. germinans* in South America are in northwestern Peru (Río Piúra, ca. 5°32′S) on the Pacific coast and in southeastern Brazil (Atafona, ca. 21°37′S) on the Atlantic coast. Like the northward limit of this species on the Pacific coast of North America, the southern distributional limit of *A. germinans* along the western coast of South America in Peru appears to have a similar cause due to the cold waters of the Humboldt Current and upwelling there (Lacerda et al. 2002).

Illustrations.— Figure 4; see also Hepper (1963: 449, fig. 309); Gibson (1970: 178, fig. 32, which is based on *Standley 87592* at F); Moldenke (1973: 151, fig. 1); Villiers (1973: 65, pl. 16); Correll and Correll (1982: 1253, fig. 540); Nash and Nee 1984: 13, fig. 2); Tomlinson (1986: 189, fig. B.8); Sanders (1997: 83, fig. 1); Proctor (2012: 586, fig. 218).

Nomenclature.— The synonymy provided above is based on types from North America and Central America or names sometimes applied to plants from these regions. Additional synonyms were listed by Moldenke (1960, 1973). Based on information provided by Stearn (1958), authorship of the combination *A. germinans* often has been attributed to "(L.) Stearn" (e.g., Tomlinson 1986; Jarvis 2007; Daniel and Figueiredo 2009). In his letter to D. Ward (17 April 1962 attached to a specimen in FLAS), Stearn indicated that the correct name for the black mangrove is *A. germinans* (L.) L., a case subsequently made by Compère (1963), and now widely accepted.

The lectotype of *Bontia germinans* at LINN also has inflorescence internodes similar to those of *A. bicolor* (i.e., ca. 4–4.5 mm long near midspike). From the image of this specimen, I have not been able to discern other diagnostic characters used here to distinguish these species. Thus, I am unable to confirm to which species it pertains.

Moldenke (1960) noted that the types of *A. nitida* and A. *tomentosa* are both *Herb. Jacquin s.n.* specimens at BM, which he annotated as such in 1936. Images of both of these very sparse specimens have been seen, and based on what is visible and available, they likely conform to *A. germinans*.

Although no specimen was designated as the type of *A. floridana* Gand., Gandoger's herbarium is at LY in France, and it is possible that the holotype is there; specimens of the type number at F, MO, Cornell, NY, and US were cited by Moldenke (1960), but he did not indicate where the holotype was located.

Local names.— "Aili sip" (Kuna; *de Nevers et al. 6554*); "arbol salado" (*Zizumbo & Colunga 500*); "black mangrove" (e.g., *Hammel 105*); "cajiel" (*Zizumbo & Colunga 500*); "istatén" (*J. González & A. Pérez 193*); "kahil" (Huave; *A. Gerardo B. 4*); "madre de sal" (*Rico-Gray & Espejel 305*); "madresal" (*Flores M. 1101*; *García B. 486*); "madre sal" (*Espejo & Hernández 2904*); "mangle de sal" (*Rico-Gray & Espejel 305*); "mangle negro" (*Chazaro B. 3299*, *Penning-*

ton & Sarukhan K. 9131); "mangle prieto" (e.g., *DIAAPROY s.n.*); "mangle pullequi" (*Moran 7151*); "mangle rojo" (*DIAAPROY s.n.*); "mangle salado" (e.g., *Arteaga et al. 130*; *Allen 5631*), "mangle senico" (*Carter 2721*); "palo de sal" (*Elorsa C. 285*); "pipi" (*Salas M. & Torres B. 825*); "puyece" (*Ferris 5396*); "puyeque" (*González O. 1131*; *Mexia 1008*); "saladillo" (*García P. & Estrada L. 1974*; *Magaña 1232*); "sahkab luk'" (*Ucán 431*); and "u najil tikin xiw" (*Tapia M. 1508*).

Uses.— Firewood (*Mexia 1008*; *García B. 486*); construction materials (*García B. 486*); and used by natives for diseases of the throat (*Choussy 1593*). Additional construction, medicinal, and food uses of the species were provided by Moldenke (1960), Burkill (1985), Cheatham et al. (2000), and Alvarez C. (2008).

Conservation.— The black mangrove is a widespread and often an abundant shrub or tree of tropical and subtropical shorelines and near coastal habitats where it is an important (often dominant) constituent of mangrove communities. Its conservation status was assessed as Least Concern (LC) by Ellison et al. (2010).

Discussion.— This species is readily distinguished by the combination of its scurfy young stems, densely spicate (headlike) inflorescences, bilaterally symmetric flowers with internally pubescent corolla lobes (Fig. 3A), styles usually conspicuously elongating near the end of anthesis or shortly thereafter as the fruits begins to form, and the grayish fruits (when dry; Fig. 3D).

Rare individuals from Mexico (e.g., *Martínez s.n.* from Baja California Sur at MEXU; *Rico-Gray 95* from Yucatán at UC) have remote nodes (to 7 mm distant, as in *A. bicolor*) near the midpoint of the spikes, but show their affiliation to *A. germinans* by their internally pubescent corolla lobes, scurfy pubescent young stems, trichomes of the rachis to 0.5 mm long, and thecae 0.8 mm long.

The fragrant flowers of *Avicennia germinans* are commonly visited by honeybees, and they are reputed to be an excellent source of honey. Corollas are often noted to be 10–20 mm long (e.g., Moldenke 1960; Tomlinson 1986). My observations concur with those of Gibson (1970), who indicated that she had seen none more than 8.5 mm in length.

Morphological variation is considerable in this species, especially with respect to habit and leaf size and shape. For example, although it is commonly a sizable tree in portions of its range, *A. germinans* becomes a dwarf shrub at the northern extent of its range in the Gulf of Mexico (Sherrod and McMillan 1985). Moldenke (1960) discussed variation in this species with respect to these and other attributes.

In a letter to Paul Standley dated 19 February 1938 (attached to *Brenes 12222* at F), Moldenke indicated that *A. tonduzii* could be "most easily" distinguished from *A. germinans* (as *A. nitida*) by the size of the flowers. Indeed some of the specimens cited and/or annotated by Moldenke as *A. tonduzii* have calyces (2–2.5 vs. 2–4) and corollas (3.5–5 vs. 4–8) that are shorter than most specimens treated as *A. germinans*. Subsequently, Moldenke (1960, 1973) distinguished *A. tonduzii* from *A. germinans* on the basis of its short (shorter than the stamens) style (vs. style exserted from the calyx when corolla is shed, surpassing the stamens) and leaf blades mostly elongate-oblong, 3–5 times as long as wide (vs. lanceolate or lance-oblong to elliptic or obovate, usually < 3 times as long as wide). Elongate styles are evident on the holotype of *A. tonduzii* at BR (and on isotypes at BR and US). The other putative distinguishing characters of *A. tonduzii* overlap those of *A. germinans* when plants from throughout the ranges of both species are considered. Tomlinson (1986) considered *A. tonduzii* as a narrow-leaved variant of *A. bicolor* and treated the name as synonymous with that species. Others have followed Tomlinson's influential account, and *A. tonduzii* has been recognized as a distinct species in some relatively recent literature (e.g., Lacerda et al. 2002).

In the southern Caribbean region and along the Atlantic coast of South America, the distribution and taxonomy of *A. germinans* become entangled with those of *A. schaueriana* Stapf & Leechman ex Moldenke. Stearn (1958) distinguished *S. schauerana* from *A. germinans* by the characters in the following couplet:

1a. Leaves mostly acute at tip; corolla lobes tomentose on both sides; style elongate . . . . *A. germinans*

1b. Leaves mostly rounded at tip, sometimes acute; corolla lobes glabrous internally, tomentose externally; style very short, the stigma nearly sessile . . . . *A. schaueriana*

Leaf tips are variable in *A. germinans*. While length of the style might be somewhat dependent on floral stage and pollination, it appears likely that styles of *A. schaueriana*, like those of *A. bicolor*, do not elongate (or at least not to the extent) as in *A. germinans*. Like *A. germinans*, *A. schaueriana* has crowded inflorescences, but pubescence of the corolla lobes would appear to be a useful character for distinguishing these species.

Representative materials examined.— **Belize**. **Belize**: St. Johns College, *J. Dwyer & R. Pippin 10030* (MO); shortcut from southern part of Belize City to Western Hwy., *A. Gentry 8560* (F); Belize, *C. Hammel 105* (K); Belize, *C. Lundell 4719* (K); W de Tropical Park, *T. Ramamoorthy et al. 3609* (MEXU); Gale's Point, just S of Bar River mouth, ca. 17°14′N, 88°18′W, *J. Ratter et al. 6560* (K); Caye Caulker (southern island), South Point, west coast, 17°43′47″N, 088°02′15″W, *J. Rietsema & D. Beveridge 19906* (NY). **Corozal**: ca. 4 km SE of Sarteneja, ca. 18°21′N, 088°07′W, *G. Davidse & A. Brant 32658* (USF); ca. 2 km S of Sarteneja, 0.5 km NE of La Isla, 18°20′19″N, 088°07′25″W, *Z. Goodwin & G. Lopez 1583* (MO). **Stann Creek**: Northeast Cay, *F. Fosberg & D. Stoddart 53854* (US); Man-O'-War Cay, W of Tobacco Cay Range, *F. Fosberg & D. Spellman 54204* (MO, US); North Silk Cay, *F. Fosberg & D. Spellman 54272* (US); Little Water Cay, *F. Fosberg & D. Spellman 54343* (F); Buttonwood Cay, *F. Fosberg & D. Spellman 54421* (US); Scipio Cay, 16°28.135′N–16°28.295′N, 088°17.793′W–88°17.829′W, *D. Lentz et al. 2355* (NY); Long Coco Caye, off Placencia, ca. 16°29.5′N, 88°12.7′W, *D. Lentz et al. 2833* (NY); Dangriga, *G. Proctor 36197* (MO); All Pines, [16°47′00″N, 88°19′00″W], *W. Schipp 625* (UC); South Water Cay, *Spellman & Stoddart 2157* (US); Seal Cay, *Spellman & Stoddart 2481* (MO); Rendezvous Cay, *Spellman & Stoddart 2498* (MO, US); Coco Plum Cay, *Spellman & Stoddart 2567* (MO, US); 4.5 km S of Southern Highway turnoff, *D. Stevenson 1132* (K). **Toledo**: W of beach road, Punto Gorda, *J. Dwyer et al. 631* (MO).

Costa Rica. **Guanacaste**: vicinity of Playa Naranjo in P.N. Santa Rosa, *F. Almeda et al. 4205* (CAS); Playa de Coco, *R. Blaisdell 300* (FSU); P.N. Palo Verde, Valle de Tempisque, Estación Catalina, Laguna Nicaragua, 10°21′10″N, 085°13′00″W, *U. Chavarría 1243* (F); Puerto Jesús, Nicoya, *O. Cook & C. Doyle 743* (US); ca. 1 km E of Río Tempisque ferry, *G. Crow 6116* (F); between Playa Comchal and Playa Brasilito, *L. Durkee 76-386* (F); Port Parker, Salinas Bay, *F. Elmore E1* (DS); Sitio Ojochal, P.N. Santa Rosa, 10°47′35″N, 85°39′00″W, *A. Fernández 315* (K, NY); Playa de Sámara, al S de Nicoya, *A. Jiménez M. 526* (F). **Puntarenas**: Golfo Dulce, vicinity of delta of Río Esquinas, *P. Allen 5631* (DS, F, FSU, US); Quepos, *F. Almeda et al. 3398* (CAS, F, NY); Cantón Golfito, Península de Osa, P.N. Corcovado, Estación Sirena, Río Corcovado, 08°28′50″N, 83°35′30″W, *L. Angulo 136* (K); Puerto Jiménez de Osa, *A. Brenes 12222* (F); Isla de Caballo, *A. Brenes 15696* (NY); Punta Morales, *J. Gomez-Laurito 9980* (F); near mouth of Río Coto Colorado, ca. 8 km S of Golfito, 08°37′N, 083°09′W, *W. Kress & L. Cablk 94-3803* (US); between Caldera and Matalimon, E of Puntarenas, *K. Lems 5026* (NY, US); cerca de Caldera, *J. León 505* (F); near Rincon de Osa, *R. Liesner 2203* (NY); vicinity of Puntarenas, *W. Maxon & A. Harvey 7841* (US); Santo Domingo, *Pittier 7109* (K, US), *7110* (F, K, NY, US); estuaires de Santo Domingo de Golfo Dulce, *A. Tonduz 10060* (DS, NY, US); N side of Estero, Puntarenas, *I. Wiggins & D. Porter 132* (CAS).

EL SALVADOR. **Ahuachapan**: Las Chacaras, La Barra de Santiago, *K. DeRiemer 1645* (US); San Francisco Menéndez, Garita Palmera, zanjón El Aguacate, 13°43′N, 090°04′W, *D. Rodríguez & E. Escobar 1875* (MO); Santuario de las Aves, 13°42′N, 90°00′W, *R. Villacorta y E. Montalvo 817* (K, MEXU). **La Libertad**: El Amatal, San Diego, 13°25′N, 089°14′W, *J. González 316* (MO); Estero de San Diego, *J. González & A. Pérez 193* (MEXU). **La Paz**: Estero de Jaltepeque, *P. Allen 7278* (US); near mouth of Río Jiboa, *F. Choussy 1593* (US); El Zapote, Costa del Sol, 13°21′N, 89°W, *J. González & M. Hernández 326* (MEXU, MO). **La Unión:** rocky beach, La Union, *A. Beetle 26263* (K, UC); ca. 1 km S of Barrancones, 13°26′08″N, 087°47′32″W, *G. Davidse et al. 37355* (MEXU, MO); coast near La Union, *V. Grant 716* (F); vicinity of La Unión, *P. Standley 20786* (US). **Sonsonate**: S of Acajutla, *P. Allen 6837* (F, US); Estero San Juan, *K. DeRiemer 1617* (US). **Usulután**: Jiquilisco, El Tercio, 13°15′N, 088°31′W, *R. Carballo & L. Cabrera 831* (LAGU-image!).

GUATEMALA. **Escuintla**: Iztapa, Canjón Morón, *M. Arrecis 106* (CAS, MEXU, MO); San José, *J. Donnell Smith 2510* (K, NY, US); San José, *W. Maxon & R. Hay 3659* (US); Had. Las Fianzas, *G. Salas 367* (US); Puerto de San José, *J. Véliz & M. Véliz 94.4076* (CAS, MEXU). **Izabal**: near Puerto Barrios, *P. Standley 72167* (F, NY). **Jutiapa**: Las Lisas, Barra el Ahumado, *M. Arrecis 74* (CAS, MEXU, MO), *121* (CAS), *122* (MEXU); Iztapa, Zanjón Morón, *M. Arrecis 105* (CAS). **Retalhuleu:** Río Ocosito en límite Tilepa, Ocós, San Marcos y Manchón, *M. Arrecis 47* (MO); Champerico, *P. Standley 66563* (F), *87592* (F, NY). **San Marcos**: Mpio Ocós, almendrales, Tilapa, *M. Arrecis 50* (MO), Ocós, *J. Steyermark 37803* (F). **Santa Rosa**: Las Lisas, *M. Lara s.n.* (MO); Las Lisas, Camaronera Mayasal, 13.80723°N, 090.21703°W, *J. López & R. Jiménez 120* (CAS); Parque de la Barra Hawaii, Aldea el Dormido, 13.84113°N, 090.34751°W, *J. López et al. 100* (CAS).

HONDURAS. **Atlántida**: ca. 5 km NE of Tela near Telatinza, ca. 15°48′N, 087°26′W, *T. Daniel & J. Araque 9478* (CAS, NY). **Choluteca**: Ratón Island, *A. Molina R. 22779* (US), *23287* (DS, F, NY, US); Cedeños Beach, *A. Molina R. et al. 31978* (F); Punta Ratón, 70 km NW de Cd. Choluteca, *C. Nelson et al. 3259* (MO). **Colón**: Río Guaimoreto, 4.5 km NE of Trujillo on road to Castilla, 15°57′30″N, 085°54′30″W, *J. Saunders et al. 625* (F, MO, NY). **Gracias a Dios**: Puerto Lempira, Laguna de Caratasca, *A. Díaz Z. 212* (MEXU); Puerto Lempira, Laguna de Caratasca, *M. Espinal 142* (MO). **Islas de la Bahía**: Isla de Barbareta, *C. Nelson & G. Cruz 8411* (US); Isla de Roatán, playa al E de Roatán, *C. Nelson & E. Romero 4591* (MO). **Valle**: cerca de Isla Zacate Grande, *D. Hazlett 916* (MO); San Lorenzo, *A. Molina R. 8635* (F); Golfo de Fonseca, Puerto Soto, 12 km from El Tular, *A. Molina R. 21454* (F, NY).

MEXICO. **Baja California**: Bahía San Francisquito [28.40814°N, 110.57079°W], *R. Moran 12625* (SD-not seen). Observed by I. Wiggins at Bahía de los Ángeles (see Turner et al. 1995). **Baja California Sur**: Playa Santispac, carr. transpeninsular, *B. Arteaga et al. 130* (MEXU); Magdalena Bay, *T. Brandegee s.n.* (DS, UC); El Mogote, peninsula extending into La Paz Bay, 24°8–11′N, 110°19–26′W, *A. Carter 2721* (DS, K, UC); Isla Carmen, vicinity of Las Salinas, ca. 25°59′N, 111°07′W, *A. Carter 5924* (UC); Isla Carmen, Puerto Balandra, ca. 26°00.5′N, 111°10.5′W, *A. Carter & R. Ferris 3733* (CAS, UC); Bahía Concepcion, ca. 14 mi S of Mulegé, *M. Dillon et al. 1954* (F); Bahía de La Paz, Chametla, 24°09′N, 110°06′W, *R. Domínguez C. 443* (MEXU); Sierra de la Giganta, ca. 12–14 mi S of Mulegé, near Bahía Santispac, *T. Elias et al. 10812* (F, NY); 16 mi S of Mulegé at Conception Bay, *R. Ferris 8680* (DS); Mpio. La Paz, Punta Prieta cerca de Pichilingue, 14 km NE de La Paz, *F. González M. et al. 8163* (MEXU); La Paz, *I. Johnston 3045* (CAS); Coronados Island, *I. Johnston 3758* (CAS, K, UC); Carmen Island, Puerto Balandra, *I. Johnston 3821* (CAS, K, UC); San Evaristo Bay, *I. Johnston 4089* (CAS, K, UC); Puerto Escondido, *I. Johnston 4293* (CAS, K, UC); Magdalena Bay, *H. Mason 1909* (CAS, DS, K);

Ballandra Bay, Carmen Island, 26°00.5′N, 111°10.5′W, *R. Moran 3926* (DS, UC), *9168* (MEXU); El Mogote, peninsula in La Paz Bay, ca. 24°10′N, 110°20′W, *R. Moran 7151* (CAS, DS, K); Concepcion Bay, *F. Shreve 7099* (F); Isla San José, costa SW, 24°54′N, 110°38′W, *M. Sousa P. 218* (MEXU); Isla del Carmen, lado W, Puerto Balandra, 26°01′N, 111°11′W, *M. Sousa P. 242* (MEXU); Magdalena Bay near Medano Amarillo, *J. Thomas 7940* (CAS, UC); Bahía Concepción, Playa Los Cocos, 26.87763°N, 111.97499°W, *D. Valvov 2005088* (MEXU); Bahía de Concepción between Mulegé and head of bay, *I. Wiggins 5455* (CAS, DS, F, UC); Estero Salinas, arm of Almejas Bay, S of Magdalena Bay, *I. Wiggins 11487* (CAS, DS, UC); 1.8 mi E of La Paz toward Pichilinque Bay, *I. Wiggins 14563* (CAS, DS); S shore of Bahía de La Paz, *I. Wiggins 16174* (DS); Puerto Escondido, 15 mi S of Loreto, *I. Wiggins 17526* (DS); N side of Bahía Astiones, W side of Isla San José, *I. Wiggins 17672* (DS); NE part of Isla San Francisco [24°50′32.36″N, 110°33′59.94″W], *I. Wiggins 17765* (DS); Bahía de la Concepción, beach at Punta Guadalupe, *I. Wiggins & D. Wiggins 18017* (DS); N side of Santispaquis Cove, Bahía de Concepción, *I. Wiggins & D. Wiggins 18239* (CAS, DS). **Campeche**: between Sabancuy and Cd. del Carmen, *R. Burnham & R. Spicer 146* (MEXU); 30 km W de Hecelchakan, camino a Isla Jaina, *E. Cabrera & H. de Cabrera 13345* (MEXU); 6 km NE de Champotón, carretera Cd. del Carmen, *E. Cabrera et al. 8497* (MEXU); Isla de Jaina, ca. 54 km W de Hecelchacan, *E. Cabrera C. et al. 11975* (MEXU); Mpio. Calkini, Isla Punta, 20°30′N, 90°W, *C. Chan V. & J. Flores 420* (XAL); “Panga” de Zacatal, *J. Chavelas P. & C. Zamora S. ES-4752* (MEXU); Mpio. Hecelchakan, 6 km antes de la costa, en la carretera de Pomuch, Isla de Jaina, 20°14′N, 090°24′W, *E. Gongora 546* (UC, XAL); Mpio. Campeche, Palmas, Cd. de Campeche, 19°52′N, 090°30′W, *C. Gutiérrez B. 5876* (XAL); Mpio. Cd. del Carmen, 5 km NE de Sabankuy, 19°03′00″N, 091°08′00″W, *C. Gutiérrez B. 7390* (MEXU); Puerto Real, *F. Menendez L. 467* (MEXU); S de Campeche, *F. Miranda 7944* (MEXU); Mpio. Calkiní, Isla Arena, 27 km de Takuché, 20°37′25″N, 090°25′W, *M. Narváez 1365* (MEXU); Mpio. El Carmen, Punta Cochinitos, Laguna San Francisco, 18°26′N, 091°46′W, *D. Ocaña N. & A. Novelo R. 158* (MEXU); carretera Champotón–Isla del Carmen, ca. 15 km de Champotón, *T. Pennington & J. Sarukhán K. 9405* (K); carretera Champotón–Campeche, *T. Pennington & J. Sarukhán K.* 9623 (K); Mpio. Champotón, camino a El Zapote, 4 km desde el entronque con la carr. Campeche–Champotón, 19°20′N, 090°45′W, *R. Rico G. 141* (XAL); 2 km N of Cd. del Carmen, *J. Sauer 2440* (F); Champotón, *W. Steere 1751* (CAS, MICH); Mpio. Tenabo, granja camaronera de Tenabo, entre KM 27 y el mar, 20°01′30″N, 090°13′06″W, *P. Zamora C. et al. 5824* (XAL); Mpio. Cd. del Carmen, Isla del Centro de Cayo Arcas, SE parte, *S. Zamudio 103* (MEXU, XAL). **Colima**: no collections seen, but species recorded from the state (see: http://www.projects-abroad.org/_downloads/uk/conservation-management-plan/mexico-conservation-management-plan-2014.pdf). **Chiapas**: Mpio. Tonalá, W side of Mar Muerto opposite Paredón, *D. Breedlove 20771* (DS); Mpio. Tonalá, E shore of Mar Muerto, N of Paredón, *D. Breedlove & R. Thorne 20806* (DS, NY); Mpio. Arriaga, balneario La Gloria, *A. Espejo & S. Hernández 2904* (MEXU); Acapetahua, cerca al Embarcadero Las Garzas, 15°12′38.7″N, 92°48′39.1″W, *H. Gómez D. 2293* (K); Las Garzas, Acapet, *E. Matuda 2728* (K, NY); Paderon, Tonala, *E. Matuda 16279* (US); Mpio. Acapetahua, 0.5 km antes de La Palma, 15°12′16, 092°48′37″W, *S. Ochoa G. et al. 4535* (MEXU); Mpio. Tonala, Col. Miguel Hidalgo, afueras de Puerto Arista, 15°55′N, 93°50′W, *V. Rico-Gray & I. Espejel 298* (F, MEXU); Mpio. Pijijiapan, Salina atras del Chocohuital, 15°30′N, 093°15′W, *V. Rico-Gray & I. Espejel 305* (MEXU, XAL); Mpio. Tapachula, Estero de Puerto Madero, 14°45′N, 092°35′W, *V. Rico-Gray & I. Espejel 346* (F, MEXU); Mpio. Puerto Madero, Puerto Madero, *E. Ventura & E. López 91* (MEXU, XAL); Las Margaritas, Pijiiapan, *G. Zavala P. & M. Illescas 19* (MEXU). **Guerrero**: Mpio. Copala, Laguna de Chautengo, *J. Almazán 248* (FCME); Mpio. Zihuatanejo, Playa La Ropa, Bahía de Zihuatanejo, 17°40′N, 101°34′W, *G. Castil-*

lo G. 1137 (UC), *6273* (MEXU, XAL); Mpio. Jose Azueta, Barra del Potosí, 17°40′N, 101°34′W, *G. Castillo C. & P. Zamora C. 6511* (XAL); Mpio. Zihuatanejo, entre la Punta Ixtapa y el Cerro El Rialito, 17°40′N, 101°39′W, *G. Castillo C. et al. 6566* (MEXU); Mpio. Cuajinicuilapa, Punta Maldonado, *N. Diego 2213* (FCME); Mpio. Acapulco de Juárez, El Arenal, Laguna de Tres Palos, *N. Diego 4161* (FCME, MEXU); Mpio. Petatlán, Cerro Huamilule, (Morro de la Laguna Potosí), *N. Diego & R. Oviedo 6636* (FCME); Mpio. Cruz Grande, W de Las Penas, *R. Fonseca 1625* (MEXU); Mpio. Cruz Grande, Los Tamarindos, Laguna de Chautengo, *R. Gutiérrez 4* (FCME); Mpio. Tecopan de Galeana, Laguna Nuxco, extremo SE, *F. Lorea 5280* (XAL); Mpio. Atoyac de Alvárez, Arenal de Palos, Laguna de Mitla, *L. Lozada P. 418* (FCME, XAL); Laguna del Potosí, *F. Menendez L. 448* (CAS); Mpio. Petatlán, 4 km de Petatlán dirección Tecpan, *A. Nuñez 605* (MEXU, XAL); Mpio. José Azueta, Cerro Huamilule, en Barra el Potosí, 17°31′56″N, 101°27′08″W, *S. Peralta 426* (MEXU, FCME); Mpio. Tecpan de Galeana, Nuxco, laguna, 17°15′07.6″N, 101°49′18″W, *S. Peralta 444* (FCME). **Jalisco**: Puerto Vallarta, *R. Acevedo R. 1487* (NY, XAL); Mpio. La Huerta, Laguna de Corte, 19°19′00″N, 104°56′20″W, *G. Castillo C. et al. 10745* (MEXU); Mpio. La Huerta, Playa Tenacatita, 19°17′00″N, 104°51′50″W, *G. Castillo C. et al. 10848* (MEXU); Mpio. Tomatlán, Playa Chalacatepec, 19°38′50″N, 105°12′20″W, *G. Castillo C. et al. 10967* (MEXU, XAL); Mpio. Tomatlán, Laguna Xola, 19°43′10″N, 105°15′20″W, *G. Castillo C. et al. 10978* (XAL); Salina al N de Chamela, *M. González G. 152* (CAS); Mpio. La Huerta, La Manzanilla, *L. de Puga 15542* (XAL); Barra de Navidad, *J. Rzedowski 14605* (DS). **Michoacán**: Mpio. Aquila, Estero de Maquili, *B. Guerrero C. 676* (XAL); Las Salinas [vic. of delta of Río Balsas, fide McVaugh 1951], *E. Langlassé 146* (K); Mpio. Coahuayana, Boca de Apiza, *C. Soto N. et al. 7116* (MEXU). **Nayarit**: Mpio. Bahía de Banderas, Bahía de Banderas, 20°47′N, 105°15′W, *G. Castillo C. 5818* (MEXU); Mpio. Bahía de Banderas, Laguna del Quelele, 20°44′N, 105°18′W, *G. Castillo C. 6012* (MEXU); Mpio. Bahía de Banderas, Club de Golf Flamingos, cerca de Bucerías, *M. Cházaro B. & R. Romero 8472* (XAL); SE of San Blas through Matanchen, SE toward Río San Cristobal, *C. Davidson 7608* (CAS); Pochote, Santiago Ixcuintla, 21°55′20.1″N, 105°30′30.9″W, *DIAAPROY S.A. de C.V. 47383* (MEXU); Tres Marías Islands, Magdalena Island, *F. Elmore 1132* (F); vicinity of San Blas, *R. Ferris 5396* (DS); Mpio. Santiago Ixcuintla, Mezcaltitán, *J. González O. 5537* (DS); Tres Marías Islands, Isla María Magdalena, *H. Mason 1793* (CAS, F, K, NY); Mexcaltitlán, *Y. Mexia 1008* (CAS, UC); Mpio. Santiago Ixcuitla, Isla de Mexcaltitán, 21°50′36″N, 105°24′42″W, *A. Miranda & G. Villegas 2053* (MEXU); Mpio. San Blas, ca. 2 mi E of San Blas on Hwy. 54, *D. Norris & D. Taranto 13329B* (CAS); Mexcaltitán, *J. Ortega 5537* (K); Isla María Magdalena, *O. Solís 9* (MEXU). **Oaxaca**: Mpio. Santa María Huatulco, Estero Cacaluta, 15°43′20″N, 096°09′40″W, *G. Castillo C. et al. 9782* (MEXU, XAL); Chacahua Bay, *F. Elmore D21a* (DS), *D22* (UC); Distr. Juchitán, Mpio. Chahuites, camino Chahuites–Las Salinas, *A. Flores M. 1101* (CAS); Mpio. Chahuites, Rancheria Trejo, *M. García B. 486* (XAL); Mpio. Huamelula, 4 km por la carr. Pochutla–Salina Cruz, 4 km después Huamelula, *J. García P. & E. Estrada L. 1974* (MEXU); Distr. Tehuantepec, Mpio. Salina Cruz, beach at La Ventosa, ca. 16°10′N, 095°09′W, *R. Gereau & G. Martin 1921* (CAS); Laguna Superior, S of Juchitán, near Xandanl, *R. King 1549* (NY, UC); Mpio. Tututepec, Chacahua, *J. Magaña 1232* (XAL); Puerto Angel, *C. Morton & E. Makrinius 2624* (K); La Ventosa Beach, ca. 6 mi E of Salina Cruz, *A. Reznicek & D. Gregory 304* (NY); Distr. Tehuantepec, Mpio. Santiago Astata, Laguna Colorada, 4 km W de Zaachilac, 15°57′39″N, 095°34′40″W, *S. Salas M. & E. Torres B. 825* (MEXU, XAL); Distr. Tehuantepec, Mpio. Salina Cruz, 500 m W de Salinas del Marquéz, 16°10′6.9″N, 095°14′24.3″W, *S. Salas M. et al. 5596* (XAL); Distr. Tehuantepec, Mpio. San Pedro Huamelula, Rancho Paraiso, 15°51′49″N, 095°50′22″W, *N. Velázquez R. et al. 265* (MEXU); Mpio. San Mateo, Huazantlán, La Salina, *D. Zizumbo & P. Colunga 500* (MEXU). **Quintana Roo**: S de Punta Allen, Cayo Cedros, Bahía de la Ascensión, *E. Cabrera 3405* (CAS, MEXU); 10 km N de Puerto Morelos, camino a Punta Caracol, *E. Cabrera & H. de Cabrera 3134* (MEXU, NY); 4 km N de la zona hotelera de Isla de Cozumel, camino a Isla de la Pasión, *E. Cabrera & H. de Cabrera 13582* (MEXU); Isla Mujeres, camino al Puerto de Abrigo, *E. Cabrera et al. 17200* (MEXU); Mpio. Isla Mujeres, Isla Mujeres, lado W de la marina, 21°19′N, 086°46′W, *C. Chan et al. 1590* (XAL); Reserva Biósfera de Sian Ka'an, 6 km E de Ramonal, *R. Durán et al. 1120* (MEXU); Mpio. Felipe Carrillo Puerto, La Laguna Xunyanche, 20°00′N, 087°40′W, *J. Flores & E. Ucan 8352* (F); Mpio. Isla Mujeres, Isla de Contoy, 21°30′N, 086°49′W, *J. Flores & E. Ucan 8855* (MEXU); Mpio. Othón P. Blanco, Cayo Centro en el Banco Chinchorro, 18°35′N, 87°20′W, *J. Flores et al. 8959* (XAL); Cozumel Island, *G. Gaumer 146* (K); Holbox Island, *G. Gaumer s.n.* (K); Cozumel Island, *E. Goldman 653* (F, US); brecha a Punta Brava al S de Pto. Morelos, *P. Moreno 843* (MEXU); Mpio. Isla Mujeres, Isla Mujeres, lado SE, 21°14′N, 086°46′W, *A. Puch et al. 865* (XAL); Mpio. Cozumel, Isla Cozumel, 20°30′N, 086°58′W, *A. Puch et al. 1073* (XAL); Mpio. Benito Juarez, camino a Punta Nizuc desde el entronque de la carretera Cancún-Chetumal, 21°N, 086°50′W, *V. Rico-Gray 123* (MEXU); Isla Mujeres, N end, *J. Sauer & D. Gade 3265* (MICH); Mpio. Lázaro Cárdenas, Chiquilá, 21°23′N, 087°23′W, *E. Ucán 431* (XAL); Mpio. Isla Mujeres, atras del Puerto de Abrigo, zona del Sak Bajo, 21°15′N, 086°45′W, *E. Ucan E. & J. Flores 1038* (MEXU, UC); Mpio. Othón P. Blanco, camino Blanco de X-Calak, rumbo a Majahual, 18°26′N, 087°56′W, *E. Ucan E. et al. 620* (MEXU); Mpio. Felipe Carrilo Puerto, Vigía Chico, Reserva de la Biósfera Sian Ka'an, *R. Villanueva 812* (MEXU). **Sinaloa**: Mpio. Escuinapa, Palmito, 9 km E al estero "Mezcal," *J. Beltrán M. 1014* (FCME); Mpio. Rosario, E edge of Mazatlán Bay, 0.7 mi W of Mex. 15, 8.6 mi N of Río del Presidio, *D. Breedlove 1577* (DS); Estero Ballena, old channel of Río Fuerte (W of Los Mochis), *R. Felger 8437* (CAS, MEXU); Topolobampo, *A. Gibson & L. Gibson 2095* (FSU); Escuinapa, Arroyo de la Codojuiz, *J. González O. 1131* (K); Mpio. Rosario, Coacoyolitos, *J. González O. 6458* (CAS); 4 km W de El Toldo, 24°57′N, 107°57′W, *V. Lopez S. 8.1* (MEXU); vicinity of Topolobampo, *J. Rose et al. 13309* (NY); vicinity of Mazatlán, *J. Rose et al. 14046* (F); N side of Topolobampo, *D. Seigler & P. Richardson 11686* (MEXU); Mpio. Los Mochis, just W of Topolobampo, 25°35′N, 109°05′W, *T. Van Devender et al. 2000-28* (NY). **Sonora**: Bahía Kino, mouth of Río de Sonora, *F. Drouet & D. Richards 3542* (F); 18.5 mi N of Bahía Kino Nuevo, *J. Hastings & R. Turner 64-35* (DS); Estero Tastiola, NW de Guaymas, *O. Holguín s.n.* (DS); Tepoca Bay, *I. Johnston 3288* (CAS); beach S of Guaymas, *G. Lindsay 1154* (DS); ca. 1 mi W of Puerto Lobos on narrow peninsula, *C. Lowe & R. Turner 3319* (DS); Sargento, *T. Mallery & W. Turnage s.n.* (DS); Guaymas, *W. Phillips 3483* (CAS) Mpio. Hermosillo, 2.7 km N of Punta Chueca, 20°02′20″N, 112°10′W, *A. Reina G. & T. Van Devender 96-635* (MEXU); Mpio. Caborca, Puerto Lobos, 30°16′16″N, 112°51′14″W, *A. Reina et al. 97-265* (MEXU); vicinity of Guaymas, *J. Rose et al. 12578* (NY); Bahía San Carlos, W of Guaymas, *Weedons M-1091* (MEXU); bayshore at Empalme, *I. Wiggins 6341* (DS); Isla Tiburón, Estero San Miguel, 28.968611°N, 112.20194°W, *B. Wilder et al. 06-276* (CAS); Isla Tiburón, Punta Tormenta estero, 29°00′51.17″N, 112°11′54.21″W, *B. Wilder et al. 08-329* (CAS); Isla Tiburón, Cyazim It, spit in estero at Punta Perla, 29.22442°N, 112.29345°W, *B. Wilder et al. 08-377* (CAS). **Tabasco**: Mpio. Frontera, Playa Boquerón, 20 km E de Frontera, *A. Guadarrama 876* (MEXU, NY); Mpio. Centla, Ejido Nuevo Centla, antes Playa Boquerón, 18°33′10.3″N, 092°30′48″W, *M. Guadarrama O. et al. 6688* (MEXU, XAL); Mpio. Nacajuca, Laguna Bayazú, llegando por el Río Gonzalez, *A. Hanan A. et al. 981* (MEXU); Mpio. Centla, Paso San Román, *F. Ventura A. 20406* (MEXU, XAL); Mpio. Paraíso, Puerto Ceiba, Isla Dos Bocas, *F. Ventura A. 20432* (XAL); Mpio. Paraíso, 4 km N de Mecoacán, *S. Zamudio R. 117* (MEXU). **Tamaulipas**: Mpio. Altamira, Barra de Chavarria S, entrada por el Barranco, *E. de Dunas 743* (XAL); 1 km W de La Pesca, cerca de la Laguna Blanca, *L. Hernández 1567* (MEXU); Mpio. Aldama, Rancho Nuevo, 23°08′12″N, 097°46′01″W, *D. Infante et al. 445* (XAL); Mpio. Matamoros, delta del Río Bravo, 25°56′56″N, 097°09′07″W, *D. Infante & J. Vázquez 656* (XAL); Mpio. Soto la Marina, campamento totuguero La Pesca, 23°47′27″N, 97°44′12″W, *E. Martínez 39316* (MEXU); Mpio. Altamira, playa cerca del Puerto Industrial, *A. Mora O. & J. Mora L. 5450* (MEXU); Mpio. Altamira/Aldama, Barra de Chavarria, *P. Moreno C. et al. 743* (MEXU); vicinity of Tampico, *E. Palmer 484* (CAS F, K, NY). **Veracruz**: Puente de Alvarado, *J. Calzada 434* (F); Mpio. Coatzacoalcos, Laguna Ostión, camino Pajapan–San Juan Volador, 18°11′N, 94°36′W, *J. Calzada 12657* (MEXU, XAL); Mpio. Panuco, alrededores de Laguna de Tamos, 22°13′N, 098°02′W, *J. Calzada et al. 6268* (XAL); Mpio. Actopan, El Morro de La Mancha, La Laguna, 19°36′N, 096°24′W, *G. Castillo C. 182* (F, UC, XAL); Mpio. Cosoleacaque, Polvorín, carretera Polvorín–Cosoleacaque, 17°59′48″N, 094°38′12″W, *G. Castillo C. et al. 14838* (MEXU, XAL); Mpio. Agua Dulce, Río Tonala, cerca de Arroyo Blasillo, *M. Chazaro B. 3299* (XAL); Mpio. Actopan, Estación Biológica El Morro de la Mancha, 19°36′00″N, 096°22′40″W, *C.M.V.A. 2* (MEXU); Mpio. Cazones, Rancho Nuevo, Estero Boquilla, *M. Cortés 455* (XAL); Mpio. Actopan, Laguna de la Mancha, carretera Cardel–Nautla, *J. Dorantes 57* (MEXU); S de Laguna Salada, *J. Dorantes et al. 1053* (F); 16 km S de Palma Sola, Laguna del Farallon [19°39′19.58″N, 96°24′40.28″W], *J. Dorantes et al. 1171* (CAS); alrededores de Laguna Verde (SW de La Planta), Alto Lucero, *J. Dorantes et al. 5132* (NY); Mpio. Alto Lucero, Lugana de San Agustín, KM 71 carretera Cardel–Nautla, 19°55′N, 096°31′W, *C. Guttierez B. 1311* (MEXU); Mpio. Zempoala, Estación de Biología "El Morro de la Mancha," INIREB, carretera Cardel–Nautla, *G. Ibarra M. 3b* (FCME); borde sur de la Laguna Salada, *A. Lot et al. 2055* (F); Mpio. Boca del Río, Mandinga, 19°03′05.52″N, 96°04′43.56″W, *F. Medina H. et al. 27* (MEXU, XAL); Laguna de Tampamochoco, cerca de Tuxpan, *A. Mendoza s.n.* (DS); Mpio. Tuxpan, 8 km de Barra de Tuxpan, *L. Monroy et al. 147* (CAS, XAL); Mpio. Actopan, 50 m SW de la boca de la Laguna de la Mancha, 19°35′N, 096°22′W, *A. Novelo 408* (XAL); Mpio. Alvarado, Laguna de Alvarado, 18°46′13″N, 095°45′38″W, *R. Palestina et al. 1460* (XAL); Laguna de Sontecomapan, *T. Pennington & J. Sarukhan K. 9131* (NY, K); Mpio. Coatzacoalcos, terracería La Barrillas–Laguna Ostión, 17°45′30″N, 094°42′07″W, *A. Rincón G. et al. 1731* (XAL); Barra de Tuxpan (20°58′N), N of Río de Tuxpan mouth, *J. Sauer & D. Gade 2981* (F); Río Coscoapan, *M. Sousa 3112* (F); Mpio. Cazones, Barra Cazones, *S. Vargas P. 90* (XAL); Mpio. Actopan, La Mancha, *F. Ventura A. 5226* (CAS). **Yucatán**: Mpio. Tizimín, 55 km en el camino a Las Coloradas, cerca el Puente del Río Lagartos, *J. Aguilar Z. & S. Diez M. 225* (MEXU); Mpio. Telchac, Laguna Rosa, 1 km de Puerto de Telchac, 21°20′N, 89°16′W, *J. Calzada et al. 6611* (F, XAL); Peña, *Chocarro & Jun 567* (BIGU); Mpio. Tizimín, 16 km E de Las Coloradas, 21°30′40″N, 87°50′15″W, *R. Durán et al. 2575* (MICH); Mpio. Hunucmá, 7.5 km E de Sisal hacia Celestún, *E. Estrada 283* (FCME); Mpio. Telchac Puerto, 2 km E de Telchac Puerto, *A. Feliciano K. 325* (MEXU); Mpio. Progresso, Isla Larga de los Arrecifes Alacranes, 22°26′N, 089°31′W, *J. Flores & E. Ucan 9253* (XAL); Alacran Atoll, S end of Perez Islet, *F. Fosberg 41866* (NY, US); Alacran Atoll, Pajaros Islet, *F. Fosberg 41904* (US); Las Bocas de Silam, *G. Gaumer et al. 23340* (F, NY, US); Progreso, *C. Lundell & A. Lundell 8140* (MEXU, MICH, NY); Mpio. Dzilam de Bravo, entre Santa Clara and Dzilam de Bravo, 21°25′N, 088°50′W, *J. Palma & R. Allkin 300* (MEXU); 6 km W de Dzilam de Bravo, brecha a Pto. Telchac, *H. Quero R. & R. Grether 2469* (MEXU); Mpio. Hunucmá, 2 km E de Sisal, 21°10′15″N, 090°00′45″W, *E. Reyes de los Santos 607* (MEXU); Sisal, *Schott 361* (F); Celestun, *Schott 473* (F); Mpio. Celestún, 8 km antes Celestún, viniendo de Kinchil, 20°53′N, 090°20′W, *V. Rico-Gray 60* (F, MEXU, UC, XAL); ca. 4 km de Sisal, viniendo de Hunucmá, Hunucmá, 21°13′N, 090°03′W, *V. Rico-Gray 75* (MEXU); Mpio. Progreso, 1.5 km S de Chelem, camino a Progreso, 21°15′N, 090°20′W, *V. Rico-Gray 87* (MEXU); 1.5 km E de Dzilam de Bravo, 21°25′N, 088°50′W, *V. Rico-Gray 95* (F, UC, XAL); Mpio. Telchac Puerto, 0.5 km S de Telchac Puerto, 21°20′N, 089°15′W, *V. Rico-Gray 101* (F, MEXU, UC, XAL); afueras de la cuidad de Río Lagartos, 21°35′N, 088°10′W, *V. Rico-Gray 106* (F, MEXU, XAL); between Progresso and Telchac Puerto, *J. Sauer & D. Gade 3207* (F); Progresso, *W. Steere 3092* (MICH); Mpio. Celestún, 1 km E de Celestún, 20°51′30″N, 090°24′00″W, *J. Tapia M. 1508* (MEXU); Tizimín, alrededores de El Cuyo, ca. 21°30′45″N, 087°40′46″W, *M. Ventura 158* (F); Alacran Reef, Isla Perez, S end of island, *B. Welch s.n.* (DUKE, MEXU).

NICARAGUA. **León**: Poneloya, ca. 12°23′N, 087°03′W, *R. Haynes 8617* (NY); 7.1 km de Las Peñitas, orillas del Estero Las Peñitas, *Sediles 408* (K); Estero Las Peñitas, 3.1 km de Las Peñitas, 12°20′N, 086°59′W, *Sediles 413* (CAS), *443* (CAS); Estero Brasil, ca. 2 km S of Hwy. 32 on road to Velero, ca. 12°10′N, 086°45′W, *D. Stevens et al. 17293* (CAS). **Managua**: Masachapa, *J. Atwood & D. Neill AN32* (NY). **Region Autonomista Atlantico Norte** (northern Zelaya): Pozo Verde, 10 km NE de Puerto Cabezas, 14°06′N, 083°20′W, *E. Little 25401* (F, US). **Region Autonomista Atlantico Sur** (southern Zelaya): Bluefields harbor, El Bluff, *S. Marshall & D. Neill 6507* (USF). **Rivas**: Estero San Juan del Sur, 11°14–16′N, 085°51–53′W, *M. Araquistain* 3809 (CAS); San Juan del Sur, *F. Seymour 1269* (MEXU, NY, UC).

PANAMA. **Bocas del Toro**: Changuinola Valley, *C. Cooper & G. Slater 81* (US); Water Valley, *H. von Wedel 987* (US). **Chiriquí**: playa cerca del KM 3, *J. Him 358* (US). **Coclé:** Aguadulce, outskirts of tidal belt, *H. Pittier 4969* (US). **Colón**: vicinity of Colón, *J. Cowell 97* (NY); vicinity of Viento Frio, *H. Pittier 4116* (US). **Guna Yala**: trail from Cangandi to dock by Mandinga airport, [09°27′39.50″N, 079°05′0.70″W], *G. de Nevers et al. 6554* (CAS, US). **Herrera**: P.N. Sarigua, 08°00′41″N, 080°29′03″W, *I. Alvarez B4339* (US). **Los Santos**: Salinas de Chitre, *W. D'Arcy & T. Croat 4200* (F). **Panamá**: Perlas Archipelago, San José Island, Naval Cove, *C. Erlanson 120* (NY); Perlas Archipelago, San José Island, *I. Johnston 1129* (US); Isla San José, *H. Kennedy 2281* (F, US); Taboga Island, Gulf of Panama, *H. Pittier 3614* (NY, US); Miraflores Locks, *W. Stern et al. 50* (US).

U.S.A. Florida: Brevard Co.: Merritt Island, *R. Kral 4972* (FSU, UC); S end of Merritt Island, Banana River, Coquina, *R. Whetstone 9116* (MO). Broward Co.: along Dania Beach Blvd., ca. 2 mi W of beach, *S. Leonard 6924* (FSU). Charlotte Co., 4.2 km S of De Soto Co. along Peace River, 2.7 km W of US 17, 26°59′50″N, 081°59′10″W, *A. Franck & B. Upcavage 1866* (USF-image!). Citrus Co.: Shell Island, near mouth of Crystal River, *R. Long 1309* (USF). Collier Co.: near Naples, *R. Godfrey 58071* (FSU); Everglades City, *O. Lakela 29824* (NY). Flagler Co.: inland waterway in vicinity of Marineland, *R. Godfrey 61686* (FSU). Franklin Co.: between St. George Sound and small tidal marsh just NE of Culpepper home on Cannonball Acres, *L. Anderson 5580* (FSU). Hernando Co.: N of Aripeka on Fla. 595, *J. Carlton s.n.* (USF). Hillsborough Co.: Long Key, *F. Lewton s.n.* (NY). Indian River Co.: along Indian River Lagoon, Oslo Riverfront East Conservation Area, Oslo Road E of US 1, ca. 3 mi. S of Vero Beach, 27°35.193′N, 080º21.902′W, *S. Myers 1281* (USF-image!). Lee Co.: Tarpon Bay, eastern Sanibel, *W. Brumbach 7904* (NY); Little Pine Island, *H. Moldenke 929* (MO). Levy Co.: causeway to Cedar Key, *R. Godfrey & P. Redfearn 52828* (UC); near jct. A Street and 3rd Street, Cedar Key, *K. Murray 80-43-10* (NY); Cedar Keys, *I. Wiggins 19342* (DS); E side of Seahorse Key, SE of lighthouse, *I. Wiggins & D. Wiggins 19430* (DS). Manatee Co.: Palmetto, *G. Nash 2450* (MO); Palma Sola, vic. of Manatee, *J. Simpson 80* (UC). Martin Co.: Jonathan Dickinson State Park (Girl Scout Camp), *R. Woodbury & R. Roberts s.n.* (USF). Miami-Dade Co.: Coral Gables, S end of Vee Lake, 25°40.5–40.7′N, 080°16.1–16.5′W, *J. Abbott 24063* (FLAS-image!); Everglades Natl. Park, Flamingo Area, 25°08.38′N, 080°55.88′W, *W. Hess et al. 8579* (MO, NY); Kampong, 4013 Douglas Road, Coconut Grove, *W. Judd 5602* (FLAS-image!). Monroe Co.: Long Key, *D. Correll & H. Correll 40150* (MO); Rode

Harbor, Key Largo, *C. Janish & J. Janish 447* (DS, MO); Big Pine Key, *W. Muenscher & R. Thorne 18073* (UC); Lower Matecumbe Key, *J. Pruski et al. 2826* (NY); Key West, just S of airport, 24°33.162′N, 081°46.024′W, *A. Salywon 1188* (CAS); E end of Packet Key, *I. Wiggins 20081* (DS). Palm Beach Co.: Jupiter Island, *G. Cooley et al. 4864* (USF). Pasco Co.: just W of Port Richey along inlet canal from beach, *J. Ray et al. 9980* (FSU). Pinellas Co., Boca Ciega, bayside just S of Treasure Island causeway, *R. Thorne 48355* (UC). Sarasota Co.: Sarasota, Marie Selby Gardens, 27°19′33″N, 082°32′28″W, *H. Bizet 51* (MO, NY); Historic Spanish Point, in Osprey W of US 41, 27°12′15″N, 082°29′46″W, *M. Nolan 62* (USF). St. Johns Co.: between Matanzas and Marineland, *R. Godfrey 70653* (CAS, FSU, GA, UC); Anastasia State Park, Conch Island, ca. 4.75 km NNW of jct. FL A1A and FL 312, E of FL A1A; immediately S of the St. Augustine Inlet, 29°53′56″N, 081°17′21″W, *J. Kunzer et al. 2146* (USF-image!); Crescent Beach, *D. Seigler & D. Young 10211* (MEXU); Anastasia State Recreation Area, NW Conch Island, S of Vilano Point and St. Augustine Inlet, UTM-471684, 3308353, *C. Slaughter et al. 16617* (FSU); Tolomato River, 30°06.618′N, 081°22.303′W, *A. Williams & S. Eastman s.n.* (USF-image!). St. Lucie Co.: Hutchinson Island, Blind Creek access area, off Indian River, *G. Silberhorn s.n.* (USF). Taylor Co., Jug Island [29°50′31.75″N, 83°36′58.05″W], *R. Godfrey 60403* (UC). Volusia Co.: 9 mi S Daytona Beach, near Ponce de Leon Inlet, *R. Norris 541* (FSU). County undetermined: Indian River, *A. Curtiss 1972* (CAS, GA, MO), *s.n.* (NY); Tampa Bay, *P. Rolfs 248* (MO). **Louisiana**: Cameron Parish: Monkey Island near mouth of Calcasieu Ship Channel at Calcasieu Pass, adjacent to ferry landing, *W. Vermillion s.n.* (LSU-image!). Jefferson Parish: Grande Isle, *J. Carlton s.n.* (USF); Fifi Island, 29.255541°N, 089.978158°W, *D. Atha 12910* (NY). Lafourche Parish: 0.6 mi S of Fourchon Road bridge (R22E, T23S, S24), *A. Lasseigne 6146* (MEXU); S of end of La. 3090, S of Fourchon City, S of Leeville, *R. Thomas et al. 103237* (MO, NY). Orleans Parish: New Orleans, *Nuttall s.n.* (K). Plaquemines Parish: ca. 40 mi (air) SSE of New Orleans, 29.40782, -89.79907, *M. Bell s.n.* (LSU-image!). St. Bernard Parish: North Islands in North Chandeleur Sound, NE of Venice, *R. Thomas et al. 89768* (MEXU). Terrebonne Parish: E end of Isle Dernier, *F. Givens 3733* (MO); Brush Island, *F. Lloyd & S. Tracy 249* (NY). **Mississippi**: Harrison Co., Bay St. Louis [possibly Hancock Co.?], *C. Sanger s.n.* (NY); Cat Island, 30.23037°N, 89.08532°W, Scheffel et al. 2014 (living plant-image!). Jackson Co.: Ranger Lagoon, Horn Island, 30.24171°N, 88.67886°W, Scheffel et al. 2014 (living plant-image!). **Texas**: Aransas Co.: Redfish Bay, causeway to Port Aransas, Rte. 361, *S. Hill 18296* (MO, NY); Port Aransas, *B. Tharp 253* (CAS, MO, NY, UC). Cameron Co.: South Padre Island, between Old Causeway and Queen Isabella Causeway, *F. Banda 81* (USF); Padre Island, just E of Port Isabel, *D. Correll et al. 25539* (UC); 8 mi SW of Port Isabel, inlet crossed by FR 1792 (NY), *J. Crutchfield 2985* (NY); Clark Island, near Boca Chica, *C. Lundell & A. Lundell 8760* (CAS, NY, UC); Point Isabel, *H. Parks 2939* (MO); bay at Boca Chica, Brazos Santiago Island, *R. Runyon 2812* (NY); Point Isabel in Lower Rio Grande Valley, *R. Runyon 5897* (UC); boca de Río Bravo, *Schott 139* (NY); Boca Chica, *G. Webster & R. Wilbur 3035* (GA). Nueces County: Aransas Pass, causeway between Aransas Pass and Port Aransas, *P. Fryxell 5162* (MEXU). Refugio Co.: near Tivoli, *J. Williams 415* (NY).

3. *Avicennia marina* (Forsk.) Vierh., subsp. ***australasica*** (Walp.) J. Everett, Telopea 5(4): 628. 1994. *Avicennia tomentosa* Sieber var. *australasica* Walp., Repert. Bot. Syst. 4: 133. 1845. *Avicennia resinifera* G. Forst., Pl. Esc. 72. 1786. *Avicennia marina* var. *resinifera* (G. Forst.) Bakh., Bull. Jard. Bot. Buitenzorg, ser. 3, 3: 210. 1921, nom illegit. (superfl.). TYPE.— Sheet 1460 in Thunberg's herbarium (lectotype, designated by Everett [1994: 628]: UPS).
Figures 1H–K, 2, 3B,D

Shrubs to 2.3 m tall. Young stems of reproductive shoots covered with dense shiny granules or scalelike projections to 0.05 m long (scurfy), soon glabrate. Leaves petiolate, blades ovate to elliptic (to obovate), 44–100 mm long, 19–41 mm wide, 1.7–2.8 (–3.6) times longer than wide, acute (to rounded or emarginate) at apex, subattenuate to attenuate at base, surfaces discolorous (abaxial lighter), punctate-pitted (sometimes inconspicuously so abaxially), adaxial surface lacking trichomes, abaxial surface covered with a dense scurfy layer. Inflorescences of axillary and terminal (sessile to) pedunculate ± headlike spikes, peduncles (0–) 1–40 mm long, scurfy or distally pubescent like rachis, rachis not or but barely visible, internodes near midspike 1–4 mm long, scurfy and pubescent with ± antrorse eglandular trichomes to 0.2 mm long. Bracts opposite, broadly ovate to triangular, concavoconvex, 3–4 mm long, abaxial surface scurfy and often pubescent like rachis. Bracteoles similar to bracts except smaller. Flowers mostly 4–16 per spike, sessile. Calyx 3.5–4 mm long, lobes elliptic to broadly elliptic, concavoconvex, imbricate, abaxially pubescent with antrorsely appressed eglandular trichomes to 0.8 mm long, margin ciliate with similar but spreading trichomes. Corollas 3.5–6.5 mm long, internally drying dark or blackish proximally and light brownish distally (those from Australasia are usually described as yellowish or orangish and the color is often darker in the corolla tube), externally glabrous (tube and base of lobes) and densely pubescent with appressed eglandular trichomes to 0.2 mm long (remainder of lobes), tube 1.5–2 mm long, limb actinomorphic, 4-lobed, lobes ovate-triangular to ovate-elliptic, 2–4.5 mm long, apically entire (or 1 lobe sometimes slightly bifid apically with division to 0.2 mm long), internally lacking eglandular trichomes (at least distally) but sometimes punctate-pitted (proximally). Stamens 4, inserted in distal half of corolla tube near base of lobes, exserted from mouth of corolla tube, oriented symmetrically (i.e., equally distant from one another) around corolla with thecae opening toward central gynoecium, 1.5–2 mm long, filaments 0.5–0.8 mm long, anthers presented at same height, thecae 1–1.2 mm long; pollen prolate spheroidal to euprolate, polar diameter (P) 28–41 µm, equatorial diameter (E) 24–27 µm, P:E = 1.04–1.75. Style not evident, stigma lobes 0.2 mm long. Fruit ovoid to subellipsoid, proximally blackish and distally light brownish when dry, 15–24 mm long, 10–19 mm across at widest expanse, pubescent with erect to flexuose to antrorse eglandular trichomes to 0.3 mm long (especially when less mature) and scurfy (especially evident when more mature). $2n = 64, 96$ (Dawson 1989).

PHENOLOGY.— Flowering: February, August–September; fruiting: February, November.

DISTRIBUTION AND HABITAT.— *Avicennia marina* has the most extensive distribution among species in the genus; it is native to eastern Africa, southern Asia, Indian Ocean and western Pacific Ocean islands, and Australia. Subspecies *australasica* occurs primarily in subtropical and temperate Australasia (i.e., southeastern Australia and northern New Zealand). It is the southernmost-occurring taxon among species of *Avicennia* in the Old World (to 38°45'S; Duke 2006), and the southernmost-occurring mangrove in the world. In southern California, where this taxon has been introduced and become naturalized (Fig. 2), plants occur in salt marshes with *Batis*, *Juamea*, *Salicornia*, *Spartina*, and *Suaeda* at or near sea level.

ILLUSTRATIONS.— Munir (1986: 1179, fig. 546); Duke (1991: 314, fig. 7); Clarke and Myerscough (1991: 285, fig. 1).

NOMENCLATURE.— The name "A. marina var. australasica (Walp.) Moldenke" has been used for this taxon, but as discussed by Everett (1994), this combination was not validly published at this rank, and other infraspecific taxa of *A. marina* are currently treated as subspecies. *Avicennia marina* subsp. *australasica* and the synonyms noted above are all based on *A. resinifera*. See Moldenke (1960) and Duke (1991) for a full list of synonyms of *Avicennia marina*.

LOCAL NAME.— Gray mangrove.

CONSERVATION.— *Avicennia marina* has been assessed as a taxon of Least Concern (LC) by Duke et al. (2010). This taxon is not native in the New World, but has become naturalized locally and is potentially invasive. On his collection *28024* made in 1979, Moran noted that plants in California had been introduced from Aukland, New Zealand about 1966–69. He also noted the presence of about 100 or more flowering-size plants plus many seedlings in the wildlife reserve where his observations were made. Initial efforts to eradicate the species were unsuccessful.

Discussion.— This species is readily distinguished from those native to the western Hemisphere by its actinomorphic flowers with yellowish to orangish corollas bearing ovate-triangular to ovate-elliptic lobes and its equidistant stamens that are inserted near the base of the corolla lobes, dehisce toward the center of the flower, and vary from 1.5–2 mm in length (Fig. 3B).

Duke et al. (1998) provided genetic evidence that supported the morphological recognition of *A. marina* as a distinct species and that supported recognition of the three infraspecific taxa (treated by him as varieties, but here recognized as subspecies): subsp. *marina*, subsp. *eucalyptifolia* (Valeton) J. Everett, and subsp. *australasica*. The latter subspecies would appear to consist of or contain polyploids based on the reported chromosome numbers of $2n = 64$ and 96 (Dawson 1989, as *A. resinifera*). These numbers suggest a possible base number of $x = 8$ or $x = 16$. A chromosome number of $2n = 36$ was reported for an unspecified subspecies of *A. marina* by Subramanian (1988; without citation of voucher). These appear to be the only recent chromosome counts for both this species and for the genus. If these numbers are accurate, both polyploidy and dysploidy would appear to have played a role in the evolution of taxa in *A. marina*. The only other known chromosome counts for *Avicennia* are $2n =$ ca. 66 and $n =$ ca. 33 by Raghavan and Arora (1958; with a meiotic figure showing $n = 33$, but without citation of a voucher) for *A. alba* Bl. Sanders (1997) indicated a base chromosome number for Avicenniaceae of $x = 18$. Although no rationale was stated for this number, his conclusion was probably based largely on Subramanian's count of $2n = 36$ for *A. marina*.

Avicennia marina subsp. *australasica* was distinguished by Duke (1991) from the other two varieties of *A. marina* by the fully (or nearly so) pubescent calyces (vs. pubescent only near the base), and the gray, fissured (vs. green, chalky smooth, and often flaky in patches) bark of the mature trunk.

Specimens Examined.— **U.S.A. California**: San Diego Co.: Northern Wildlife Preserve, North Mission Bay, tidal area 100 m W of Rose Creek, 32.7949°N, 117.2247°W, *I. Kay 29* (UCR); E edge of Kendall/Frost Marsh, Mission Bay, San Diego, ca. 32˚47.5′N, 117˚13.8′W, sea level, 9 September 1979, *R. Moran 28024* (CAS, GH, MEXU, NY, UC, US); same locality, 12 June 1990, *R. Moran 31036* (CAS, JEPS).

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